ECOLOGICAL INTERACTIONS BETWEEN ZOOPLANKTON AND PHOTOSYNTHETIC BACTERIA IN CRAWFORD LAKE, ONTARIO.

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ABSTRACT

The present study was carried out to test the hypothesis that photosynthetic bacteria contribute a large portion of the food of filter feeding zooplankton populations in Crawford Lake, Ontario. The temporal and spatial variations of both groups of organisms are strongly dependent on one another.

By using ^{14}C-labelled photosynthetic bacteria, the ingestion and clearance rates of *Daphnia pulex*, *D. rosea*, and *Keratella* spp were estimated during summer and fall of 1982. These quantitative estimations of zooplankton ingestion and clearence rates on photosynthetic bacteria comprised an original addition to the literature. Photosynthetic bacteria comprised a substantial portion of the diet of all four dominant zooplankton species. The evidence for this is based on the ingestion and clearance rates of the dominant zooplankton species. Ingestion rates of *D. pulex* and *D. rosea* ranged from 8.3×10^5 to 14.6×10^5 cells.ind.$^{-1}$ hr^{-1} and 8.1×10^5 to 13.9×10^5 cells.ind.$^{-1}$ hr^{-1}. Their clearance rates ranged from 0.400 to 1.000 ml.ind.$^{-1}$ hr.$^{-1}$ and 0.380 to 0.930 ml.ind.$^{-1}$ hr^{-1}. The ingestion and clearance rates of *Keratella* spp were 600 cell.ind.$^{-1}$ hr^{-1} and 0.40 ul.ind.$^{-1}$ hr^{-1} respectively. Clearance rates were inversely proportional to the concentration of food cells and directly proportional to the body size of the animals.

It is believed that despite the very short regeneration times of photosynthetic bacteria (3-8 hours) their population densities were controlled in part by the feeding rates of the dominant zooplankton in

Crawford Lake. By considering the regeneration times of photosynthetic bacteria and the population clearance rates of zooplankton, it was estimated that between 16 to 52% and 11 to 35% of the photosynthetic bacteria were consumed by Daphnia pulex and D. rosea per day.

The temporal and spatial distribution of Daphnia pulex, D. rosea, Keratella quadrata, K. cochlearis and photosynthetic bacteria in Crawford Lake were also investigated during the period of October, 1981 to December, 1982. The photosynthetic bacteria in the lake, constituted a major food source for only those zooplankton which tolerate anaerobic conditions. Changes in temperature and food appeared to correlate with the seasonal changes in zooplankton density. All four dominant species of zooplankton were abundant at the lake's surface (0-4m) during winter and spring and moved downwards with the thermocline as summer stratification proceeded.

Photosynthetic bacteria formed a 2 m thick layer at the chemocline. The position of this photosynthetic bacterial layer changed seasonally. In the summer, the bacterial plate moved upwards and following fall mixing it moved downwards. A vertical shift of 0.8m (14.5 to 15.3m) was recorded during the period of June to December. The upper limit of the photosynthetic bacteria in the water column was controlled by dissolved oxygen, and sulfide concentrations while their lower limit was controlled by light intensity. A maximum bacteriochlorophyll concentration of 81 mg $Bchl.l^{-1}$ was recorded on August 9, 1981. The seasonal distribution of photosynthetic bacteria was controlled inpart by the grazing of zooplankton. Other factors associated with zooplankton grazing were oxygen and sulfide concentrations.

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INTRODUCTION

A. MEROMICTIC LAKES

Meromictic lakes are lakes in which some water remains partly or wholly unmixed within the main water mass during the circulation period (Hutchinson 1967). The term "meromictic" was coined by Findenegg (1935) in an attempt to describe some Australian lakes which never mixed to the bottom. Since then, numerous reports which are described below have been published on different aspects of meromictic lakes. However, only a few of them considered the biological aspects of meromixis. This is of great interest, however, because the permanent stagnation of water below the chemocline results in complete oxygen depletion, and the accumulation of sulfides in the monimolimnion. This in turn, results in an unusual biological assemblage of organisms at the chemocline.

Goehle and Storr (1978) for example found that the major biological activity in the meromictic Devil's hole lake took place at the chemocline. The environment at the chemocline is particularly well suited for the growth of photosynthetic bacteria (Sorokin 1969,1970; Takahashi and Ichimura 1969; Parkin and Brock 1981b). In addition, there is a strong relationship between the biology and chemistry of the chemocline layer. A detailed study of this unique environment should therefore be of value in determining the basic interactions among its biological components. For example, the role of photosynthetic bacteria in the aquatic food chain and its relationship to the temporal

and spatial distribution of zooplankton would be of great importance to understanding the ecology of meromictic lakes.

B. PHOTOSYNTHETIC BACTERIA IN FRESHWATER ECOSYSTEM

i) Organic Matter Producers

In meromictic lakes, an appreciable part of the organic matter is produced either photosynthetically or chemosynthetically via the action of the sulfur bacteria in conjunction with sulfide oxidation in the chemocline (Matsuyama and Saijo 1971). Ogino and Takesi (1978) in an attempt to evaluate the nutritive value of photosynthetic bacteria mentioned that their dry weight contains 43.7 per cent crude protein with a caloric value of 5.3 Kcal/g dry weight. This is comparable to that of rotifers (Ibid). Culver and Brunskill (1969) emphasized that the localized mineralization of organic matter by photosynthetic bacteria in the chemocline keeps the nutrients in the euphotic zone, which would otherwise be lost to the sediments.

ii) Primary Producers

In recent years, several assessments of primary production of photosynthetic bacteria have been carried out in order to determine the importance of these bacteria as primary producers in stratified lakes (Takahashi and Ichimura 1968; Sorokin 1970; Gorlenko et al 1978; Parkin and Brock 1981b). Parkin and Brock (1981b) in their study on Knaack Lake found a very low contribution (3.3 to 5.7 per cent) of photosyn-

thetic bacteria relative to the total primary production within the lake. However, the primary production of photosynthetic bacteria in that lake was found to be high during the ice cover period. By way of contrast, Culver and Brunskill (1969) reported that photosynthetic bacteria in the meromictic Fayetteville Green Lake were responsible for up to 81 per cent of its total annual primary production. A contribution of 46 per cent has been reported by Lawrence et al (1978) for Waldsea Lake. Hammer (1981) emphasized the importance of photosynthetic bacteria in the total primary production of saline lakes. The highest contribution (91 per cent of the daily production and 82.3 per cent of the annual production) was attributed to photosynthetic bacteria by Cohen et al 1977. Severn (1982) reported that photosynthetic bacteria made a substantial contribution (up to 60 per cent) to the overall primary production of the Crawford Lake.

iii) The Aquatic Food Chain

Besides the importance of photosynthetic bacteria as a producer of organic matter, they have been reported as a potential food source for zooplankton (Severn 1982). Culver and Brunskill (1969) and Sorokin (1970) suggested that photosynthetic bacteria are heavily grazed by zooplankton. Normal development of copepod nauplii when fed on a pure culture of Chlorobium has been reported by Gophen et al (1974). They also mentioned that the preference of Ceriodaphnia for Chlorobium was more than for algal diets. In Lake Kaiike, Japan, Matsuyama and Shirouzu (1978) found that green sulfur bacteria at the chemocline seem

to be an important food source for zooplankton. This was also reported by others (Northcote and Halsey 1969; Sorokin 1969; and Walker 1975). Sorokin (1969) in an excellent report showed that Chlorobium was an effective food source for zooplankton. He also suggested that the production of zooplankton in Lake Belovod was mainly supported by the photosynthetic bacteria and not the phytoplankton.The aggregation of zooplankton at the chemocline suggested that the photosynthetic bacteria were a probable food source (Takahashi and Ichimura 1968; Larsson 1971; Guerrero et al 1978).

iv) Spatial Distribution

Northcote and Halsey (1969) noted that the position of the bacterial plate in Mahoney and Lyons Lakes in British Columbia increased in depth as light penetration and the depth of the mixolimnion increased. According to these authors, the magnitude of the vertical shift in the bacterial plate was limited by the availability of light, H_2S, and CO_2. Parkin and Brock (1981a) reported a diel movement of photosynthetic bacteria and explained it as an effect of sulfide concentration. Light intensity is the limiting factor controlling the depth to which the photosynthetic bacteria can exist, while sulfide and dissolved oxygen concentration define the upper limits of the photosynthetic bacteria growth zone (Takahashi and Ichimura 1969; Hammer 1981; Steenbergen and Korthals 1982). In contrast, Culver and Brunskill (1969) mentioned light was the only controlling factor associated with seasonal and spatial variation of

Fayetteville Green Lake photosynthetic bacteria. Almost all of the previous reports mentioned photosynthetic bacteria as completely anaerobic, whereas figures from Matsuyama and Shirouzu (1978) and Goehle and Storr (1978) showed the availability of bacteria at a depth where oxygen concentration varied from 0.1 to 4.5 $mg.l^{-1}$.

C. ZOOPLANKTON IN THE AQUATIC FOOD CHAIN

Cladocerans, and rotifers are considered to be important in the aquatic ecosystems in terms of density, biomass, production, grazing, and nutrient regeneration (Hutchinson 1967; Haney 1973a; Porter 1977; Makarewicz and Likens 1979). Bogdan and Gilbert (1982) reported that the recycling of nutrients by zooplankton is necessary for the high phytoplankton production rates during the summer months.

i) Seasonal and Spatial Distribution

Numerous reports have been published on the vertical and seasonal distribution of major zooplankton species in both stratified and non-stratified lakes (e.g. Melville and Maly 1981; Edmondson and Litt 1982; Gerritsen 1982) whereas only a few of them are on meromictic lakes (Northcote and Hasley 1969; Matsuyama and Shirouzu 1978; Swift and Hammer 1979). Among the cladoceran zooplankton populations in general, low populations in winter and near absence among the aestival species can be observed (Wetzel 1975). Their population increases from overwintering adults or resting eggs with rising temperatures in spring

and early summer. Whereas rotifers are cold stenotherm, and exhibit maxima in winter and spring (Wetzel 1975). However, he also mentioned that their seasonal distribution varies greatly among different lakes. In general, seasonal population fluctuations of zooplankton are strongly related to temperature variations, most strongly of all in Keratella sp.(Edmondson 1965; George and Fernando 1975).

Swift and Hammer (1979) found no live zooplankton below the chemocline and those few found were dead or moribund. Most of the Daphnia were above 5m and did not make any appreciable diel change in position. Matsuyama and Shirouzu (1978) mentioned that vertical water motion is generally restricted in stratified lakes, so that zooplankton can readily congregrate at a depth favorable to their growth. They also suggested that photosynthetic bacteria may play an important role in determining the characteristic vertical distribution of zooplankton in meromictic lakes. Temperature (Hutchinson 1967; Wetzel 1975; Gerristen 1982), oxygen (Fox et al 1951), and food (Haney 1973a; Bogdan and Gilbert 1982) have been reported to be the major controlling factors determining the temporal and spatial variation of zooplankton populations.

ii) Filter Feeding

Much of the organic matter contained within a lake ecosystem exists at some time in the form of tiny particles, such as algae, bacteria, detritus, and organic aggregates. The most common form of

food gathering in this aquatic environment is filter feeding, i.e.,the passage of water through specialized appendages which retain all or a portion of the suspended particulate matter (Haney 1973b). The ingestion of small, short-lived, highly productive, easily ingested and digested algal cells by highly productive rotifers may be a major pathway of energy in lake systems (Makarewicz and Likens 1979; Bogdan and Gilbert 1982). Sorokin (1969) reported that photosynthetic bacteria are a better food source than algae because bacteria are more easily ingested and digested.

Knowledge of zooplankton filter feeding is vital in interpreting the major flow of energy and matter in aquatic systems. Quite a number of reports are available on the filter feeding of major zooplankton species on different types of food such as, algae (Nauwerck 1959; Haney 1973a; Bogdan and Gilbert 1982; Porter et al 1982), yeast (Rigler 1961; Burns 1968), and bacteria (Paterson et al 1978; Starkweather et al 1979). No such reports on the filter feeding of zooplankton on photosynthetic bacteria have yet been published. The works that could be considered as the only reports on the feeding of zooplankton on photosynthetic bacteria have been those by Sorokin (1969) and Matsuyama and Shirouzu (1978). Some reports of zooplankton feeding on photosynthetic bacteria are based on indirect observations,such as 1) the congregation of zooplankton at the chemocline (Takahashi and Ichimura 1968; Culver and Brunskill 1969; Northcote and Halsey 1969; Larsson 1971), 2) the pink color of their gut (Goehle and Storr 1978; Swift and Hammer 1979), 3) the inverse relationship of bacteria and zooplankton populations (Guerrero et al 1978), and 4) the spectro-

photometric analysis of zooplankton gut contents (Severn 1982). However, no information is available on the quantitative estimation of filtering rates of zooplankton on photosynthetic bacteria.

The main concern with the experiments on filter feeding has been to determine the capabilities of zooplankton to fulfil their nutritional requirements. According to Haney (1973b), Nauwerck (1959) was the first to study the filter feeding of zooplankton on mixed populations of phytoplankton. Since then, the study of zooplankton filter feeding and their ingestion rates for different food types has received a great deal of attention. However, most of the studies have been restricted to laboratory experiments (e.g. McMahon and Rigler 1965; Burns and Rigler 1967; Starkweather et al 1979) where many important ecological variables cannot be simulated. To overcome these problems, some attempts were made to determine the filtering rates in nature (Haney 1973a; Gulati 1978; Paterson et al 1978; Bogdan and Gilbert 1982). It soon became apparent that filtering rates for a single zooplankton species were variable and were influenced by a number of critical factors, such as 1) body size of the animal (Haney 1973a; Haney and Hall 1975; Hall et al 1976; Paterson et al 1978), 2) concentration of food (Gulati 1978; Starkweather et al 1979; Bogdan and Gilbert 1982), 3) size and shape of food particles (Gliwicz 1969; Starkweather and Gilbert 1978; Bogdan and Gilbert 1982), 4) variation of temperature (Nauwerck 1959;Haney 1973a), 5) oxygen concentration (Heisy and Porter 1977), 6) active rejection of food particles (Burns and Rigler 1967), and 7) chemical nature of food (Starkweather and Gilbert 1978).

Downing and Peters (1980) emphasized the effects of food concentration and body size since these two factors were shown to have a large effect on filtering rates in laboratory experiments (Burns and Rigler 1967; Burns 1968). However, demonstration of their effect was rare in the field (Haney 1973a; Haney and Hall 1975). They also mentioned that calculation of filtering rates in the field was less straightforward than in the laboratory because in the field there might be additional food sources other than the labelled one. McMahon and Rigler (1965) found that above a certain concentration of food cells, feeding rates of Daphnia magna were no longer proportional to concentration but remained constant. They showed that the relationship between the concentration of food and feeding rate of D. magna was similar for a variety of food types. According to these authors these lower rates were probably due to lower retention of the smaller bacterial cells. Similar reports on crustaceans and rotifers have been published by Gliwicz (1969). Starkweather et al (1979) mentioned that ingestion rates were strongly density dependent, reaching maximal values at the highest food densities tested.

iii) Measuring Filtering Rates: Isotope Methodology

The measurement of filtering rates of various zooplankton on a natural food suspension was first attempted by labelling the entire nannoplankton with ^{14}C by adding $NaH^{14}CO_3$ to lake water that had been filtered through a fine bolting silk to remove larger zooplankton and net plankton, reintroducing particular species of zooplankton, and determining their uptake of radioactivity (Nauwerck 1959). Problems

inherent in this method were: 1) the lack of assurance that all components of the nannoplankton were equally labelled with ^{14}C, 2) the excessively long experimental period during which significant egestion may have occurred, and 3) the absence of other zooplankton species and phytoplankton forms which may influence the filtering rates (Haney 1973b).

Burns and Rigler (1967) determined the filtering rates of Daphnia rosea in natural lake waters by adding small quantities of highly radioactive yeast cells to unfiltered lake water. Haney (1973a) suggested that if the animals begin feeding immediately and feed thereafter, the rate of food particle ingestion should extrapolate to zero activity at zero feeding time. He also mentioned that the inflection point of the uptake curves indicated that the gut-passage time for both Daphnia galeata and D. rosea approximated 5 minutes. This agrees well with the estimates of Bond (1963 in Haney 1973a) for Daphnia galeata (4 min.) and Burns and Rigler (1967) for D. rosea (6-7 min.). Matsuyama and Shirouzu (1978) reported 8 min. gut-passage time for Daphnia sp. fed photosynthetic bacteria from Lake Kaiike, Japan. Bogdan and McNaught (1975) measured the rate of radioactive uptake by Daphnia and Diaptomas feeding on ^{14}C labelled phytoplankton and found that the radioactivity of zooplankton increased linearly during 0-10 minutes, then began to decrease progressively. They explained this decrease as the beginning of the egestion of labelled food. Haney (1973a) mentioned that gut-passage time or egestion time is influenced by the species, their size, the ambient temperature, and the amount of food present. He noted that smaller species have shorter egestion times

than larger species.

Bogdan and McNaught (1975) suggested that one of the necessary conditions for measuring filtering rates is that the feeding period should be shorter than the gut-passage time. Rigler (1961) mentioned that the use of radioactive food to measure filtering rate proved to be a satisfactory method. He showed that the errors inherent in the method are small and can be corrected. It was found by Rigler that the largest errors were due to excretion of ingested tracer and a rapid initial uptake of radioactive food. Neither was greater than 3 per cent.

D. PURPOSE OF THE STUDY

The objective of the present investigation was to test the hypothesis that photosynthetic bacteria in meromictic Crawford Lake make an appreciable contribution to the diet of the major filter feeding zooplankton. As there have been no reports published on the quantitative estimation of zooplankton ingestion and clearance rates for photosynthetic bacteria, this investigation constitutes an original addition to the scientific literature. To test the hypothesis noted above, in situ ingestion and clearance rates were measured using ^{14}C tracer techniques (Matsuyama and Shirouzu 1978). Some additional information such as temporal and spatial variation of photosynthetic bacteria and major zooplankton species (Daphnia pulex, D. rosea, Keratella cochlearis, and K. quadrata) were necessary in order to estimate the seasonal relationship between photosynthetic bacteria

and zooplankton. Seasonal changes of the major limnological parameters such as dissolved oxygen, temperature, specific conductivity, and light intensity were also estimated in order to characterize the system.

The small meromictic Crawford Lake was chosen for study because: 1) meromictic lakes generally contain a large population of photosynthetic bacteria and filter feeding zooplankton, 2) the small size of this single basin lake facilitated obtaining representative measurements, and 3) the lake is also relatively protected from the activities of man.

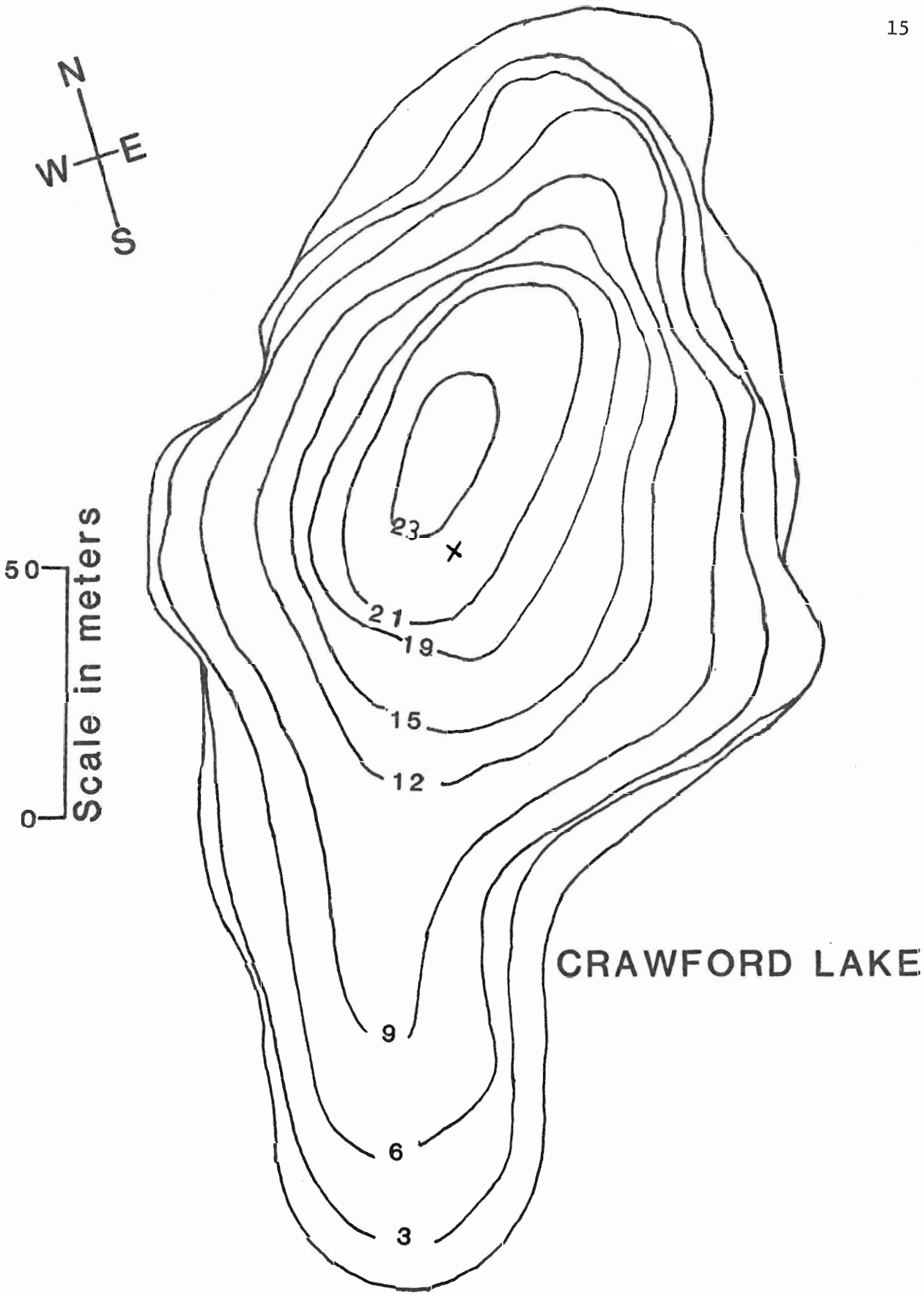
Once the rate of consumption of photosynthetic bacteria by each zooplankton (e.g. rotifers, cladocerans) was estimated, it was possible to use this information to generalize to the lake as a whole. In order to do this, changes in the seasonal abundance of each of the major zooplankton species had to be estimated. In addition, the vertical distribution of each of these taxa was determined because it was felt that only a portion of the vertically distributed population would be actively feeding at the lake's chemocline where the anaerobic bacteria were concentrated.

E. DESCRIPTION OF THE LAKE

Crawford Lake (Fig.1) is situated on the Niagara Escarpment, Ontario,(43° 28 N, 79° 5 W) at an elevation of 156 meters above mean sea level. The lake displays a steep sided conical morphometry with a mean depth and maximum depth of 10.3 and 23 meters respectively. The lake

covers an area of 22000 sq.meters (Severn 1982). It has one inflow at the north end and one outflow at the south end. The lake is well protected from the wind by the surrounding deciduous-coniferous forest and the high dolomite cliffs. A more complete description of the lake was provided by Dickman and Severn (in press).

Figure 1. Contour map of Crawford Lake with one sampling station indicated by X. (after Prepas and Rigler 1978).


N
W
E
S
Scale in meters
50
0
23
21
19
15
12
9
6
3
CRAWFORD LAKE

MATERIALS AND METHODS

A. MEASUREMENTS OF LIMNOLOGICAL PARAMETERS

Four major limnological parameters were measured during the present investigation (October, 1981 to December, 1982). Measurements of these parameters were necessary to characterize the lake and the influence of meromixis on the vertical distribution of dominant zooplankton species and photosynthetic bacteria. Parameters included were water temperature, light intensity (May to December, 1982), specific conductivity, and dissolved oxygen. These parameters were used to determine the precise depth of the chemocline and the bacterial plate.

Measurements of limnological parameters were made from a single station (Fig.1) twice each month at 1 meter intervals from the lake's surface to a depth of 20 meters. Careful attention was given to the maintainence of a consistent sampling procedure during the entire period of investigation. Specific conductivity in micro $mhos.cm.^{-1}$ was measured using a YSI Model 33 Conductivity Meter. The same meter was used to measure the temperature in ^{o}C and these data were used to correct specific conductivity to 25 ^{o}C. An Oxygen Meter (YSI Model 51A) was used to measure the concentration of dissolved oxygen in $mg.l.^{-1}$ at 1m intervals down the length of the water column. Dissolved oxygen as $mg.l.^{-1}$ was then converted to per cent saturation of dissolved oxygen.

Light intensity was measured in μEn.m^{-2} s^{-1} by a photochromatic Light Meter (Li-Cor,Inc. Model LI-158B). On some sampling dates it was not possible to measure some parameters particularly dissolved oxygen and specific conductivity (less than 5% of the total) due to instrument failure at freezing temperatures.

B. COLLECTION AND ENUMERATION OF ZOOPLANKTON SAMPLES

Zooplankton samples were collected from a single station near the center of the lake (Fig.1). Samples collected over 2 meter intervals from the surface to 20 meters depth with a Birge-Juday closing net (32 cm diameter and 68 micron mesh size). At each 2m depth interval, the plankton net was pulled up exactly 2 meters and closed by dropping a messenger. During each sample tow, 141 liters of water passed through the net. Closing net samples were concentrated into a 250 ml container secured at the cod end of the net. Samples were preserved in 4% buffered formalin solution and transported to the laboratory for identification and enumeration. It was assumed that Brige-Juday closing net was 100% efficient in filtering water through it.

A Leitz (Diavert) Inverted microscope at 250X magnification was used for identification and enumeration. Zooplankton were identified to species following Brooks (1957), Ward and Whipple (1966), and Chengalath et al (1971). On the first few sampling dates all the samples were enumerated by counting five 10 ml subsamples. Mean values

were calculated as individuals per cubic meter of water. Later, when it was attempted to calculate the 95 per cent confidence limits, large variations were found among the replicate counts. As a result the enumeration procedure was changed. The entire sample was concentrated into 10 ml by centrifuging and the whole sample was counted. Only the 4 dominant species (Daphnia pulex, D. rosea, Keratella quadrata, and K. cochlearis) were counted. Variation among 3 replicate samples was estimated on one occasion. Among the 20 samples only 4 showed 5 to 10% variations and less than 5% variations were observed among the rest of the samples.

C. COLLECTION AND ESTIMATION OF BACTERIOCHLOROPHYLL

During the period of May, 1982 to December, 1982, samples were collected from the chemocline depth (14-16 m) in order to study the vertical distribution and seasonal changes in the abundance of photosynthetic bacteria[1]. The abundance of photosynthetic bacteria was measured in mg bacteriochlorophyll per liter of water. On all sampling dates (except May,1982) samples were collected at every 10th of a meter from 14 to 16 meter depths. A pump sampler employing 20 m of plastic tubing of 2.5 cm internal diameter was used to collect samples from the desired depths. Samples collected were filtered through a 68 micron mesh plankton net to remove the zooplankton. These were stored in 500 ml dark brown pyrex bottles and transported to the laboratory for further preparations. On the same day of collection, three 50 ml

1. The dominant form was Chlorobium phaeobacterioides (Montesinos 1983).

subsamples from each 500 ml sample were filtered through 0.45 micron Millipore filters. The Millipore filters with their concentrated photosynthetic bacteria on them were dried and kept in the dark until the spectrophotometer was ready for operation. Bacterioclorophyll pigments were extracted in 30 ml of an acetone:methanol:distilled water solution (80:15:5; Daley et al 1973). When the extractions were completed, filters were removed and the samples were analysed spectrophotometrically. On the first day of analysis it was found that the acetone solution bleached the chlorophyll and thus lowered the absorbance values in the spectrophotometer. This problem was resolved by reducing the amount of time between extraction and analysis. Following this observation the rest of the analyses were done within 2 minutes of extraction. An Aminco DW-2 UV/VIS Spectrophotometer was used for these analyses. Variation in bacteriochlorophyll concentrations among the three subsamples was minimal. However, the mean values were calculated to express the actual concentrations. The absorbance values were converted into mg Bchl per liter of water following the equation of Takahashi and Ichimura (1968):

mg (Bchl)654/liter= 10.2 X D X F

D= Absorbance at 654 nm.

F= (Extracted volume) / (Filtered volume).

10.2= Extinction coefficient for Bchl at 654 nm.

Bacteriochlorophyll concentrations at every 10th of a meter were used to estimate the vertical distribution of these bacteria. Peak (maximum) concentrations among the vertical samples on different sampling dates were used to compare the seasonal changes in the abundance of the photosynthetic bacteria.

D. METHODOLOGY FOR ZOOPLANKTON FEEDING ON PHOTOSYNTHETIC BACTERIA

Feeding of zooplankton especially Daphnia pulex and D. rosea, on photosynthetic bacteria was conducted on five sampling dates (June 13, 27, July 25, August 09, and October 15). The experimental procedures were similar to those of Matsuyama and Shirouzu (1978) with certain modifications such as i) incubation under water; ii) anesthesizing zooplankton before preservation; iii) washing the zooplankton with distilled water, 1 % HCl, and 0.85 % NaCl solutions before preparation for the scintillation counter. Consecutive steps for the entire experiment are described below.

i) Incubation of photosynthetic bacteria with $NaH^{14}CO_3$

Water containing photosynthetic bacteria was collected using a pump sampler.These bacteria were incubated with ^{14}C. The rapid attenuation of light by the dense bacterial plate was used to determine its location. This water was filtered through a 68 micron mesh plankton net to remove zooplankton. Samples were stored in 8-liter incubation bottles. The incubation bottles were kept covered using a black bag to protect the photosynthetic bacteria from light shock at high light intensity. Water in the incubation bottles was incubated with 50 ml of 10 micro curie $NaH^{14}CO_3$ solution. Then the incubation bottles were lowered down to the depth from which the initial sample

was taken. The normal incubation period was 4 hours (10 am to 2 pm). After incubation, water with ^{14}C-labelled photosynthetic bacteria was used for the zooplankton filtration studies.

ii) Incubation of zooplankton with ^{14}C-labelled photosynthetic bacteria

Zooplankton samples for incubation with ^{14}C-labelled photosynthetic bacteria were collected about 10 to 15 minutes before the 4-hour incubation period described above had elapsed. Samples for these experiments were collected from the same depth as that from which photosynthetic bacteria had been collected following the same procedure mentioned earlier for zooplankton collection. Collected samples were filtered through a 68 micron mesh net to remove the unlabelled photosynthetic bacteria.

Dark brown (opaque;500ml) pyrex bottles were used as feeding chambers. Seventeen such bottles were arranged in a row and were further shaded by dark black polyethelene bags. Each bottle was filled with incubated water containing ^{14}C labelled photosynthetic bacteria. The time series of the feeding experiments were 0,1,2,....15,16 minutes. Zooplankton collected in one sample tow were released into each feeding bottle containing ^{14}C labelled photosynthetic bacteria. After the prescribed time interval of feeding the zooplankton in each bottle were anesthesized with lime water (Prepas and Rigler 1978) and were preserved in 4 per cent buffered formalin. Zooplankton in each

feeding bottle was preserved separately and brought to the laboratory for radioactivity measurements.

iii) Determination of radioactivity of the zooplankton

In the laboratory zooplankton in each feeding bottle was separated into respective species. Each group of species was washed in 25 ml of distilled water, 25 ml of 0.85 per cent NaCl, and 25 ml of 1 per cent HCl. This washing was done to remove the ^{14}C which may have been adsorbed to their body surfaces. Then 10 specimens of each species were placed in a scintillation vial containing 5 ml of Tissue Solublizer (N.C.S. Amershamsearl). After 7 days, 10 ml of Organic Scintillation Cocktail (O.S.C. Amershamsearl) was added. Three vials for each species and each time interval were prepared for scintillation counting. These vials were placed in the dark for 72 hours. After a second storage in dark each vial was placed in the Scintillation Counter (Searle, Delta 300, Liquid Scintillation System). Each vial was counted for 20 minutes. Scintillation Counter reading (cpm) for each vial were corrected for background and quench (number of specimens of each species) in the following way:

cpm/species = (cpm - B)/G

cpm= Radioactivity in counts per minute

B = Background

G = Number of specimens of particular species in each vial.

The mean value of the three vials for each species and each feeding time was used for the actual radioactivity. Additional experiments were

done on one occasion to see the effect of the undissolved body shell of *Daphnia* sp. on the radioactivity measurements. For this purpose, increasing numbers of unlabeled specimens were placed in scintillation vials containing the same quantity of $NaH^{14}CO_3$ solution. Different vials containing increasing number (1 to 10) of *Daphnia* showed a variation of $\pm.80$ cpm.ind^{-1}. from the minimum of 1 specimen to maximum 10 specimens.

iv) Measurement of filtering rates of individual species

The inflection in the feeding curve of increasing feeding time against radioactivity was interpreted as the gut-passage time or egestion time (Haney 1973b). Thus the radioactivity at the inflection time was used to calculate the filtering rates. For the measurement of filtering rates, it was necessary to estimate the concentration of photosynthetic bacteria and from this the radioactivity per single bacterial cell in the initial incubation bottle was calculated. During each experiment, the remaining sample in the incubation bottle was brought to the laboratory. Photosynthetic bacteria were counted using a haemocytometer. Initially a Leitz (Diavert) Inverted microscope at 1250X magnification was used. Later, epiflorescence was installed. Concentrations of bacterial cells were expressed in number of cells per ml of water. To measure the radioactivity of single bacterial cells, three 100 ml subsamples from the initial incubation bottle were filtered through 0.45 micron Millipore filters. Then the filters were dissolved in 5 ml of Tissue Solublizer. After 4 days, 10 ml of liquid scintillation cocktail was added to each vial containing the dissolved

subsample filter. Radioactivity of the photosynthetic bacteria per ml of water was measured by the scintillation counter. The number of bacterial cells per ml of water was compared with the cpm per ml of water to calculate the radioactivity for single bacterial cells. Filtering rates of the two species of Daphnia was calculated as ingestion rates (number of cells.ind.$^{-1}$ hr.$^{-1}$) and clearance rates (ml of water.ind.$^{-1}$ hr.$^{-1}$). Bogdan and Gilbert's (1982) equations were used to calculate the ingestion rates and clearance rates. The equations are:

$$\text{Ingestion Rates (\# of cells.ind.}^{-1}\text{ hr.}^{-1}\text{)} = \frac{\text{cpm/ind. X 60 minutes}}{\text{cpm/cell X feeding time}}$$

$$\text{Clearance Rates (ml of water.ind.}^{-1}\text{ hr.}^{-1}\text{)} = \frac{\text{\# of cell/ml of water}}{\text{Ingestion Rates.}}$$

$$\text{PCR (liters.(inds/cu.m).}^{-1}\text{ day}^{-1}\text{)} = \text{ICR X PD X 24 hours.}$$

PCR = Population Clearance Rate

ICR = Individual Clearance Rate

PD = Population Density (ind./cu.m.)

The results of the temporal and spatial variations of zooplankton and photosynthetic bacteria and the feeding estimates of zooplankton on those bacteria are described in the next section.

RESULTS

A. LIMNOLOGY OF THE LAKE

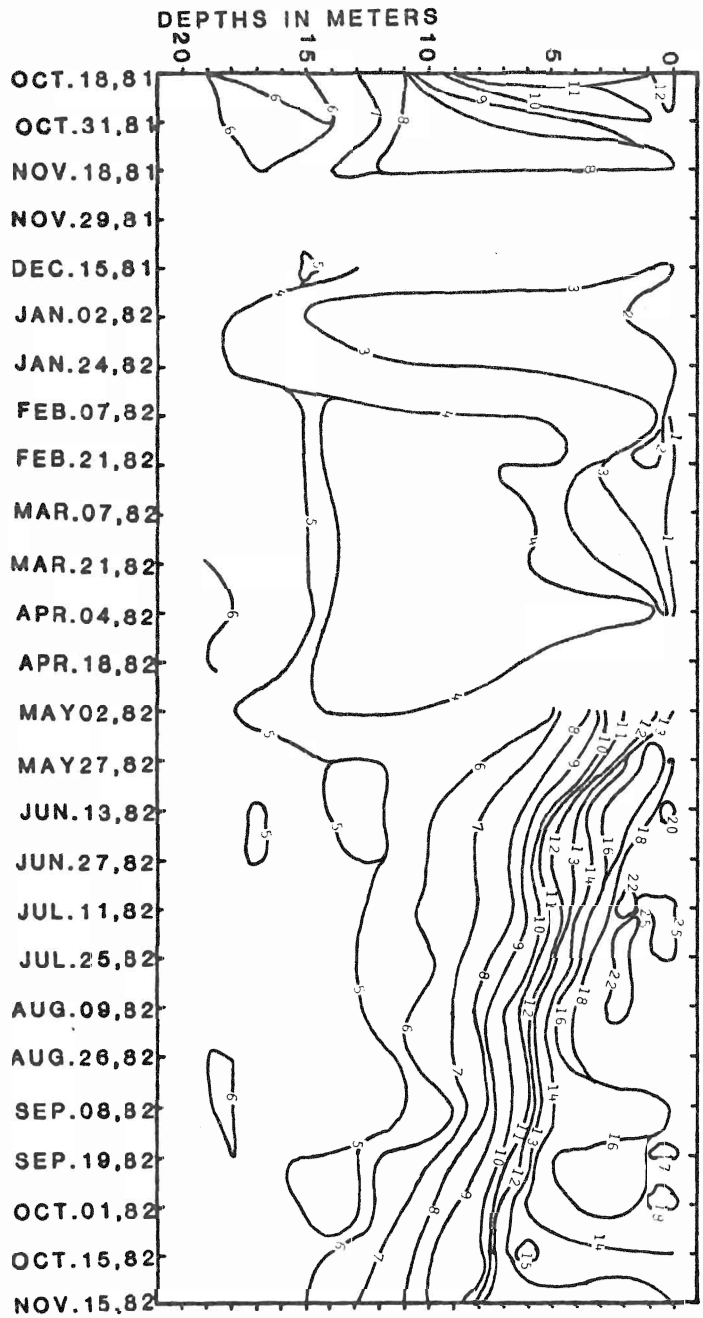
The regular sampling of Crawford Lake and the length of time (October, 1981 to December, 1982) over which the present investigation was carried out have demonstrated that the lake is distinctly meromictic.

i) Temperatures in Crawford Lake

Seasonal temperature profiles in Crawford Lake (Fig.2) demonstrated the typical thermal patterns of a meromictic lake. Surface water temperature varied from 0.8 °C in February to 25 °C in July. Temperature at the chemocline (14-16m) ranged from 2.8 °C in January to 6.9 °C in October, however, in the summer months the range was much narrower (4.8 to 5.7 °C). Below the chemocline (17-20m) temperature varied from 3.8 °C in January to 6.4 °C in November.

Adeabatic heating was consistently noted in Crawford Lake (Figs.5-7). This pattern of increasing temperature as a function of monimolimnetic depth is characteristic of meromictic lakes. Similar temperature profiles have been reported by Hammer et al (1978) in Waldsea Lake. Wetzel (1975) explained that the higher temperatures in the monimolimnion were due to bacterial metabolism. While Cole (1979) explained that it was due to back radiation in deep lakes and direct solar radiations in shallow meromictic lakes. In Crawford Lake it was possibly due to both geothermal and biogenic influences.

Figure 2. Isotherm diagram of temperature as a function of depth and time (Temperature in degree centigrade).


DEPTHS IN METERS
20
15
10
5
0
OCT.18,81
OCT.31,81
NOV.18,81
NOV.29,81
DEC.15,81
JAN.02,82
JAN.24,82
FEB.07,82
FEB.21,82
MAR.07,82
MAR.21,82
APR.04,82
APR.18,82
MAY02,82
MAY27,82
JUN.13,82
JUN.27,82
JUL.11,82
JUL.25,82
AUG.09,82
AUG.26,82
SEP.08,82
SEP.19,82
OCT.01,82
OCT.15,82
NOV.15,82

ii) Light Attenuation in Crawford Lake

Vertical differences in light attenuation during the period of May to November are shown in Table 1. The percentage attenuation of light as a function of depth is shown in Table 2. A Major portion (82-97%) of the surface light intensity were attenuated in the top 5 meters. It was also observed that during the summer months, light attenuation in the top 5 meters was higher than in late spring. This can be attributed mainly to the absorption of light by the phytoplankton (Ganf 1974). Maximum amount of light attenuation (97%) on July 25 was coincident with the algal bloom (interpreted from the oxygen supersaturation) during that time (Table 2).

Below 10 meters, light attenuation was very low and ranged from 1 to 3 per cent of the surface light intensity (Table 6). Only 1 to 6 $\mu En.m.s^{-2}\ ^{-1}$ light intensity penetrated to a depth of 14 meters (Table 1). The light intensity below 14 meters was always less than 1 per cent of the incident surface light intensity. At 15 meters depth, light intensity ranged from 0.002 $\mu En.m.s^{-2}\ ^{-1}$ on August 26 to 3 $\mu En.m.s^{-2}\ ^{-2}$ on June 27. This rapid extinction of light at 15 meters was attributed to the absorption of light by the dense layer of photosynthetic bacteria in Crawford Lake.

iii) Specific Conductivity profiles in Crawford Lake

Seasonal changes in the specific conductivity profiles are shown

Table 1. Summer and fall light intensity downwelling profiles in Crawford Lake (light intensity in uEn.m.$^{-2}$s^{-1}).

Depths in m →	0	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16
Dates																	
May 27	973	973	233	219	170	122	78	68	66	32	24	19	13	8	6	2	0.10
Jun.13	973	488	365	245	183	110	86	49	37	24	18	13	8	6	4	2	0.01
Jun.27	665	446	219	198	159	132	90	60	41	31	21	14	10	7	5	3	0.80
Jul.11	352	213	120	76	57	38	29	20	15	10	6	3	2	0.95	0.43	0.22	<.001
Jul.25	804	584	180	75	46	26	17	12	9	7	5	4	2	2	1	0.12	0.03
Aug.09	1141	854	488	330	232	110	103	61	35	24	17	10	7	5	4	0.002	<.001
Aug.26	781	437	317	219	81	73	61	39	27	17	13	8	5	2	1	0.02	0.002
Sep.08	973	365	244	219	119	83	60	44	29	21	14	8	5	2	0.17	0.01	<.001
Sep.19	973	488	293	204	166	100	66	37	22	16	10	7	5	3	3	0.01	<.001
Oct.03	781	219	171	98	66	51	34	24	15	11	7	5	3	2	0.61	0.12	0.02
Oct.15	357	200	130	92	42	38	25	18	11	9	5	3	2	1	0.54	0.02	<.001
Nov.15	310	184	98	71	35	28	24	16	10	9	4	3	3	1	0.51	0.02	<.001

Table 2. Percentage attenuation of surface light intensity as a function of depth.

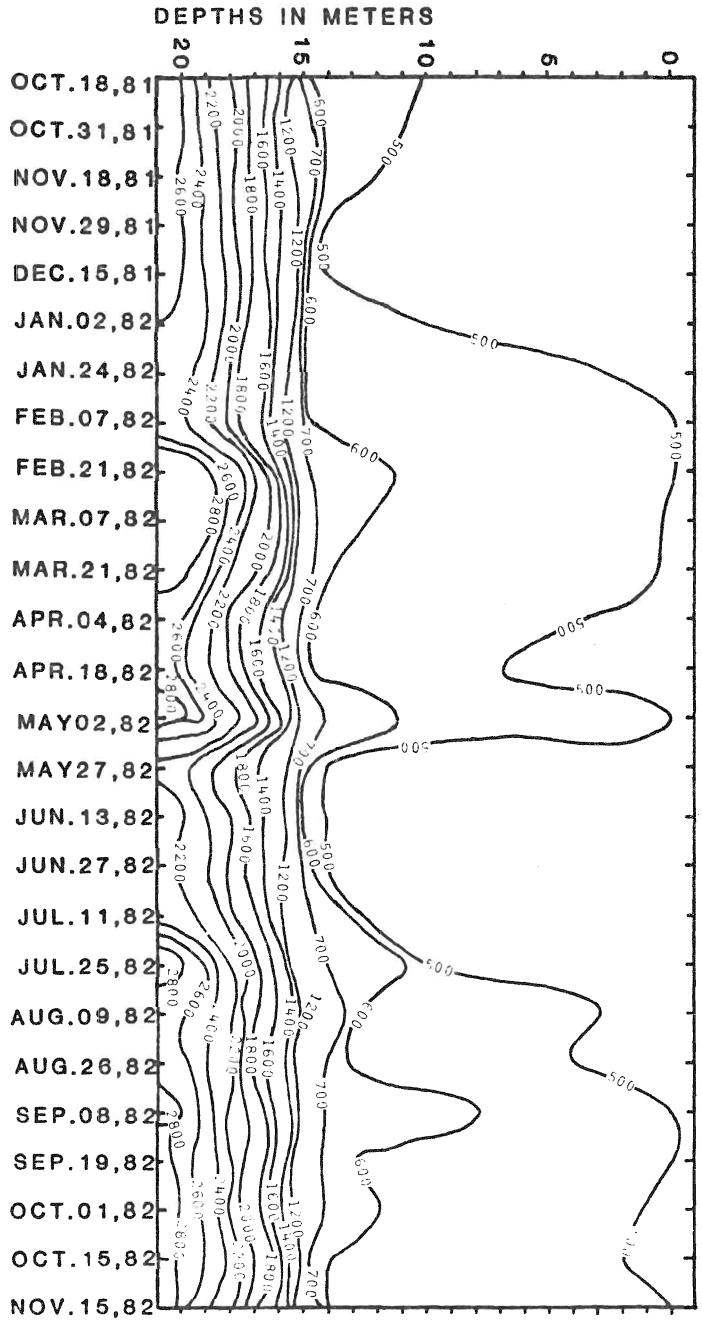
Depths in meters	0-5	5-10	10-15	Per cent of surface light intensity available at the chemocline at 14 meters	at 15 meters
May 27,82	87 %	10 %	3 %	0.62 %	0.21 %
Jun.13,82	89 %	09 %	2 %	0.40 %	0.21 %
Jun.27,82	82 %	16 %	2 %	0.75 %	0.45 %
Jul.11,82	89 %	09 %	2 %	0.12 %	0.06 %
Jul.25,82	97 %	02 %	1 %	0.12 %	0.01 %
Aug.09,82	90 %	08 %	2 %	0.35 %	0.0002%
Aug.26,82	90 %	08 %	2 %	0.12 %	0.002%
Sep.08,82	91 %	07 %	2 %	0.02 %	0.001%
Sep.19,82	90 %	09 %	1 %	0.31 %	0.001%
Oct.01,82	93 %	06 %	1 %	0.08 %	0.011%
Oct.15,82	89 %	09 %	2 %	0.15 %	0.006%
Nov.15,82	91 %	08 %	1 %	0.16 %	0.006%

in Fig.3. During the entire period of investigation, the vertical profile of specific conductivity showed a similar pattern. This pattern is characteristic of most meromictic lakes (Hammer et al 1978).

Specific conductivity from the surface to a depth of 14 meters showed very little changes. Exceptions to this generalization occurred mainly during the summer months when an approximate increase of 70 to 100 $umhos.cm^{-1}$ was recorded between 3 and 7 meters (Figs.6-7). This increase corresponds to the zone of maximum phytoplankton dissolved oxygen. Algal cells at high density may enhance the electric current carrying capacity of water and thereby increase the water's conductivity.

Specific conductivity increased rapidly below 14 meters and increased gradually below 16 meters (Fig.3). The pattern of gradual incraese of conductivity in the monimolimnion remained approximately the same throughout the entire period of investigation (Figs.5-7). A sharp secondary chemocline usually 1m thick has been reported by Hammer et al (1978) in Waldsea Lake which was not observed in Crawford Lake. However, the conductivity in the monimolimnion was not constant and varied within the year. Minimum and maximum monimolimnetic conductivity were recorded during June and July-August respectively. Similar shifts in conductivity have been reported by Northcote and Halsey (1969) in the meromictic lakes of British Columbia. The reason for these shifts was not clear. Hammer et al (1978) mentioned that it was associated with a record rainfall, but no correlation between rainfall and increased conductivity was observed in Crawford Lake.

Figure 3. Isobar diagram of temperature corrected specific conductivity (micro mhos/sq.cm) as a function of depth and time.


DEPTHS IN METERS
20
15
10
5
0
OCT.18,81
OCT.31,81
NOV.18,81
NOV.29,81
DEC.15,81
JAN.02,82
JAN.24,82
FEB.07,82
FEB.21,82
MAR.07,82
MAR.21,82
APR.04,82
APR.18,82
MAY02,82
MAY27,82
JUN.13,82
JUN.27,82
JUL.11,82
JUL.25,82
AUG.09,82
AUG.26,82
SEP.08,82
SEP.19,82
OCT.01,82
OCT.15,82
NOV.15,82

iv) Dissolved oxygen profiles in Crawford Lake

The upper mixolimnion was always saturated with dissolved oxygen (Fig.4). Saturation down to maximum depth of 14 meters was observed in late November, 1981 (Fig.5). This was associated with fall mixing. At the same time in 1982, the lake was saturated with oxygen only to 9 meters (Fig.5). By early December, 1982, the dissolved oxygen saturation was observed at 12 meters. Thus the lake appears to have mixed oxygenated water into the thermocline nearly one month early in 1983 due to strong wind action and homothermal condition during November (Fig.8)

During the summer and fall of 1982 supersaturations occurred in the mixolimnion. Supersaturation was first observed on July 25 at 5 meters. This was associated with the first summer algal bloom of the year (Fig.6). Supersaturation increased in concentration and the zone of supersaturation moved downward during the late summer and early fall to a depth of 9m. Supersaturation depths were associated with thermocline depths.

Dissolved oxygen was depleted rapidly from the lower mixolimnion with increasing depth and was completely depleted at the top of the chemocline (14m). In summer and early fall, oxygen depletion in the mixolimnion was comparatively more severe and the top of the anoxic layer moved up from 15 meters in late July to 12 meters in mid November just before fall mixing (Figs.6-7). This severe oxygen depletion can be explained by the great quantities of dead and dying organic matter

Figure 4. Isobar diagram of per cent saturation of dissolved oxygen as a function of depth and time.

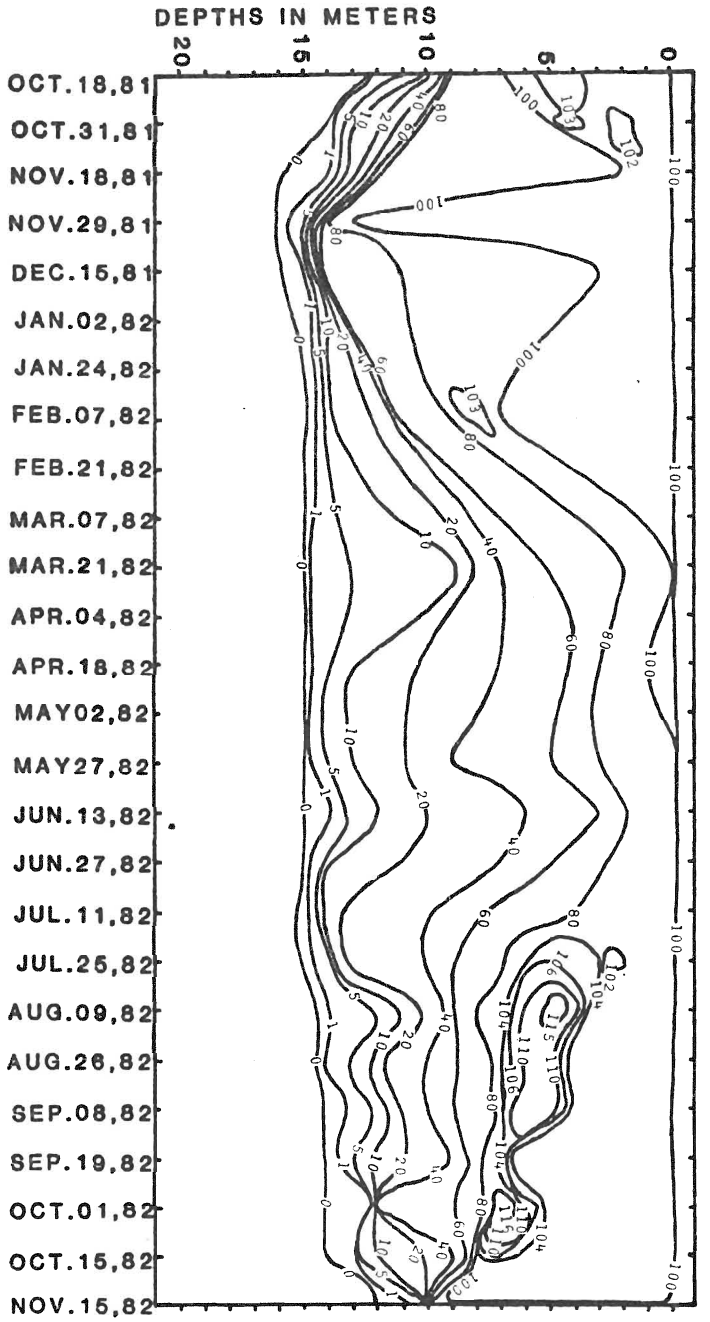

DEPTHS IN METERS
20
15
10
5
0
OCT.18,81
OCT.31,81
NOV.18,81
NOV.29,81
DEC.15,81
JAN.02,82
JAN.24,82
FEB.07,82
FEB.21,82
MAR.07,82
MAR.21,82
APR.04,82
APR.18,82
MAY02,82
MAY27,82
JUN.13,82
JUN.27,82
JUL.11,82
JUL.25,82
AUG.09,82
AUG.26,82
SEP.08,82
SEP.19,82
OCT.01,82
OCT.15,82
NOV.15,82

Figure 5. Temeprature (•·····•), Specific Conductivity (⊙——⊙), and Dissolved Oxygen (•——•) profiles in Crawford Lake (October 18, 1981 to March 21, 1982).

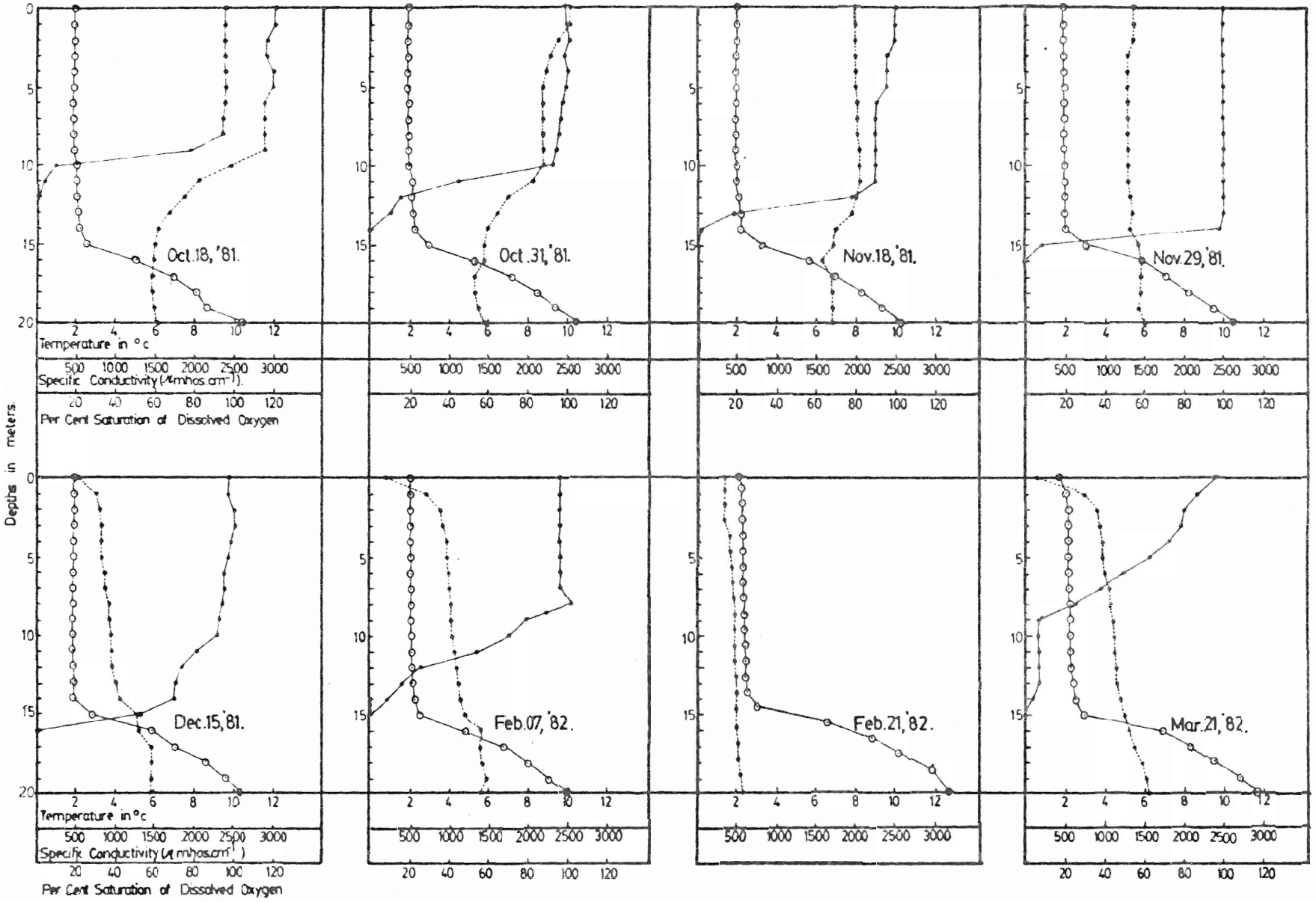

Depths in meters
Oct.18, '81.
Oct.31, '81.
Nov.18, '81.
Nov.29, '81.
Dec.15, '81.
Feb.07, '82.
Feb.21, '82.
Mar.21, '82.
Temperature in °c
Specific Conductivity (μmhos.cm⁻¹).
Per Cent Saturation of Dissolved Oxygen

Figure 6. Temperature (•-------•), Specific Conductivity (⊙———⊙), and Dissolved Oxygen (•———•) profiles in Crawford Lake (April 4, 1982 to July 25, 1982).

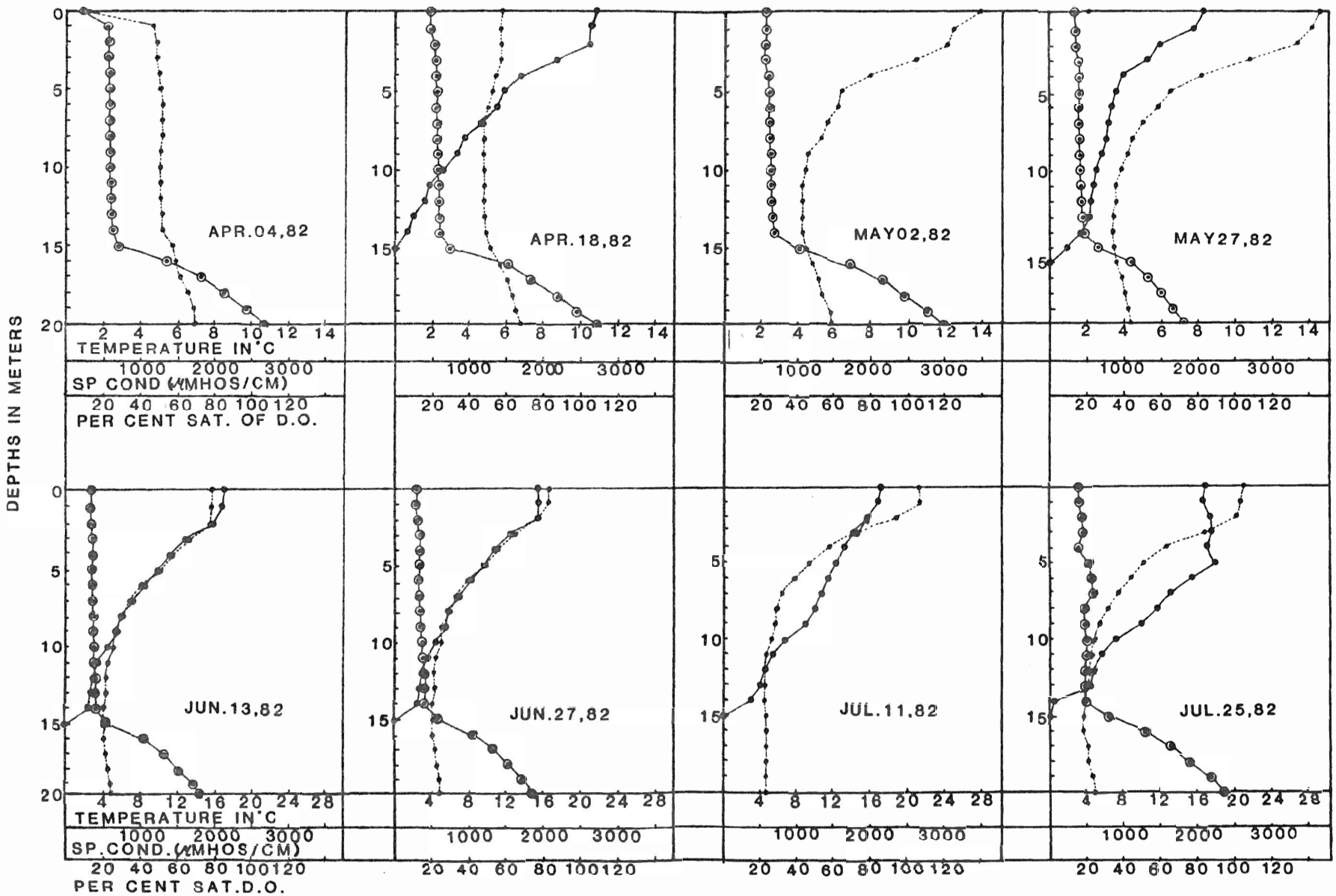
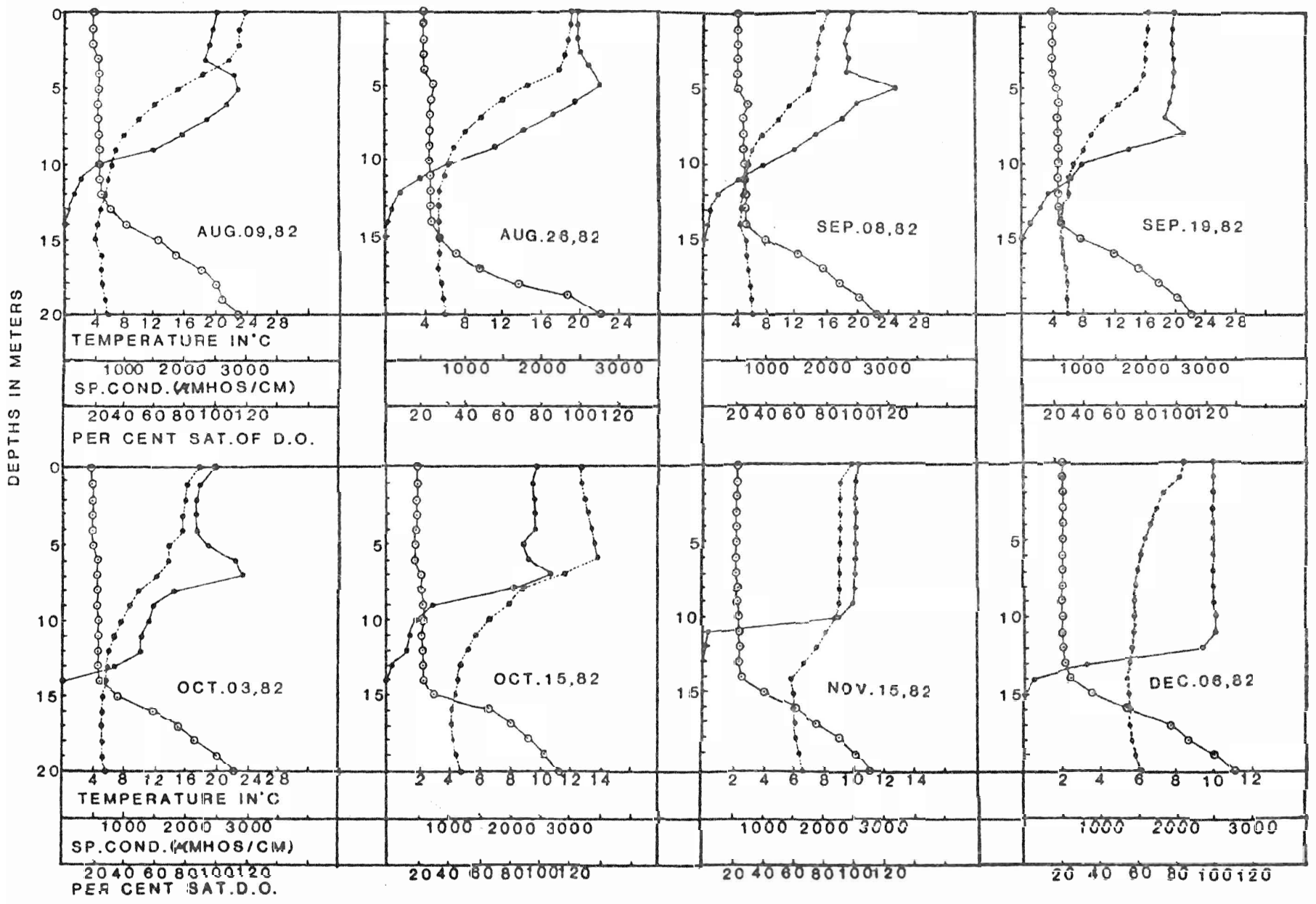

DEPTHS IN METERS
APR.04,82
APR.18,82
MAY02,82
MAY27,82
JUN.13,82
JUN.27,82
JUL.11,82
JUL.25,82
TEMPERATURE IN °C
SP COND (μMHOS/CM)
PER CENT SAT. OF D.O.
SP.COND.(μMHOS/CM)
PER CENT SAT.D.O.

Figure 7. Temperature (•--------•), Specific Conductivity (⊙———⊙), and Dissolved Oxygen (•———•) profiles in Crawford Lake (August 9, 1982 to December 6, 1982).


DEPTHS IN METERS
AUG.09,82
AUG.26,82
SEP.08,82
SEP.19,82
OCT.03,82
OCT.15,82
NOV.15,82
DEC.06,82
TEMPERATURE IN°C
SP.COND.(μMHOS/CM)
PER CENT SAT.OF D.O.
PER CENT SAT.D.O.

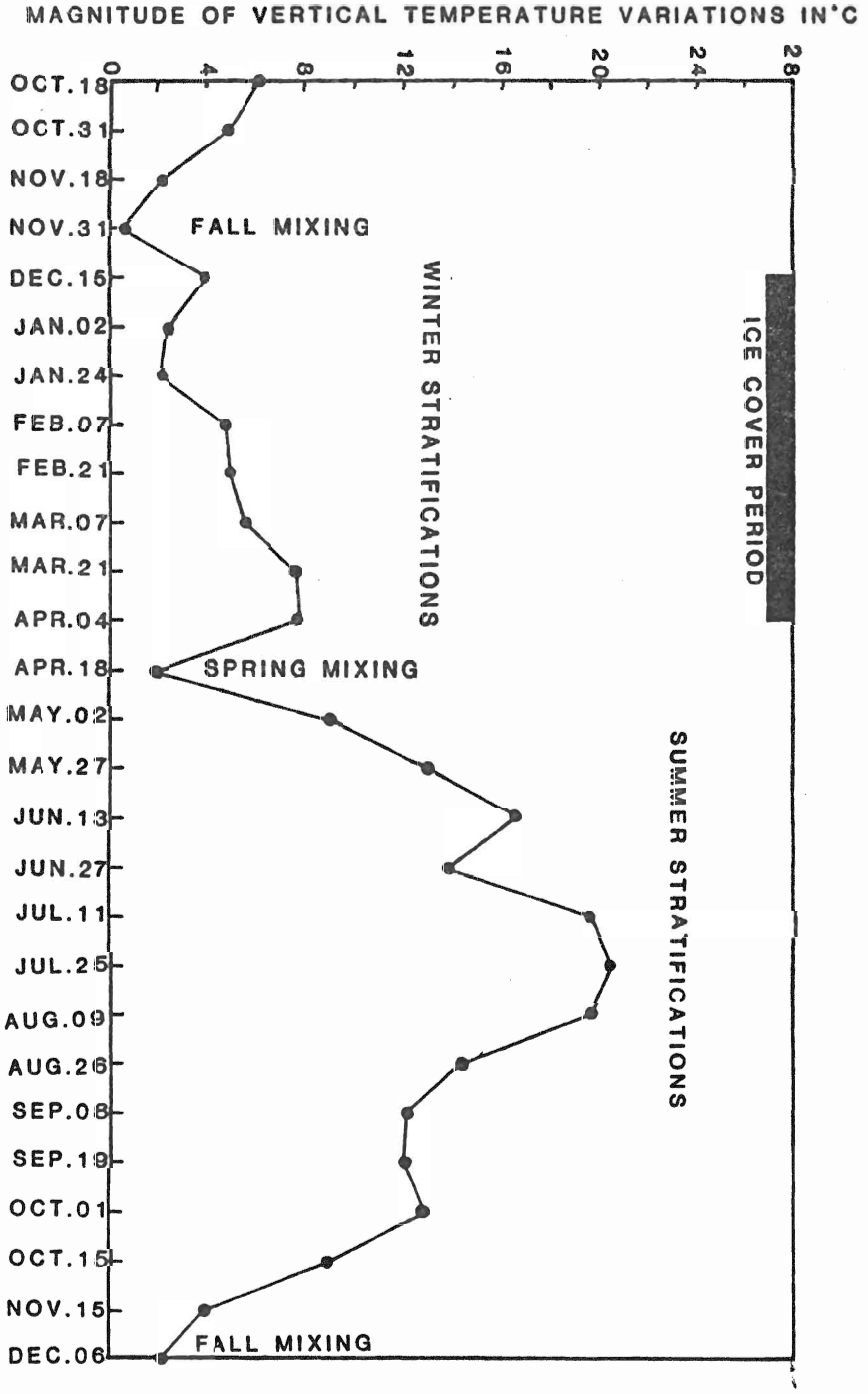
which removes the oxygen in the lower mixolimnion (Dickman and Artuz 1978). During the fall mixing in November, 1981, the top of the anoxic layer went down to 16 meters (Fig.5). An isothermal temperature profile was evident during that time (Fig.8).

v) Location of the chemocline in Crawford Lake

The precise location of the chemocline in a meromictic lake depends on which parameter is chosen to define the chemocline depth. Attempts were made to locate the chemocline depth by the depth of O_2-H_2S boundary. As the depth of this boundary varied during the year and did not demonstrate the same depth of abrupt increase of conductivity, it was believed to be misleading to use oxygen depletion as a parameter to locate the chemocline depth. King and Tyler (1982) reached the similar conclusion.

Specific conductivity was found to demonstrate the best suitability for locating the precise depth of the chemocline. During the entire study period the mixolimnion increased abruptly in conductivity (Figs.5-7). Moreover, the conductivity profiles were not affected by the shifting environmental conditions. King and Tyler (1982) mentioned that for their lake specific conductivity depth profiles were gradual rather than abrupt and hence they were not justified to use conductivity in their study. However, in Crawford Lake, specific conductivity profiles were always abrupt rather than

Figure 8. Seasonal changes in the magnitude of vertical temperature variations in Crawford Lake (horizontal bar represents the ice-cover period).


MAGNITUDE OF VERTICAL TEMPERATURE VARIATIONS IN°C
0
4
8
12
16
20
24
28
OCT.18
OCT.31
NOV.18
NOV.31
DEC.16
JAN.02
JAN.24
FEB.07
FEB.21
MAR.07
MAR.21
APR.04
APR.18
MAY.02
MAY.27
JUN.13
JUN.27
JUL.11
JUL.25
AUG.09
AUG.26
SEP.08
SEP.19
OCT.01
OCT.15
NOV.15
DEC.06
FALL MIXING
WINTER STRATIFICATIONS
ICE COVER PERIOD
SPRING MIXING
SUMMER STRATIFICATIONS
FALL MIXING

gradual, and there was never any problem in locating the precise depth of the chemocline on any sampling date. According to King and Tyler (1982) the thermal profiles give a hint of the location of the chemocline when the top of the monimoimnion is warmer than the lower mixolimnion.

B. TEMPORAL AND SPATIAL DISTRIBUTION OF DOMINANT ZOOPLANKTON SPECIES

i) Daphnia pulex

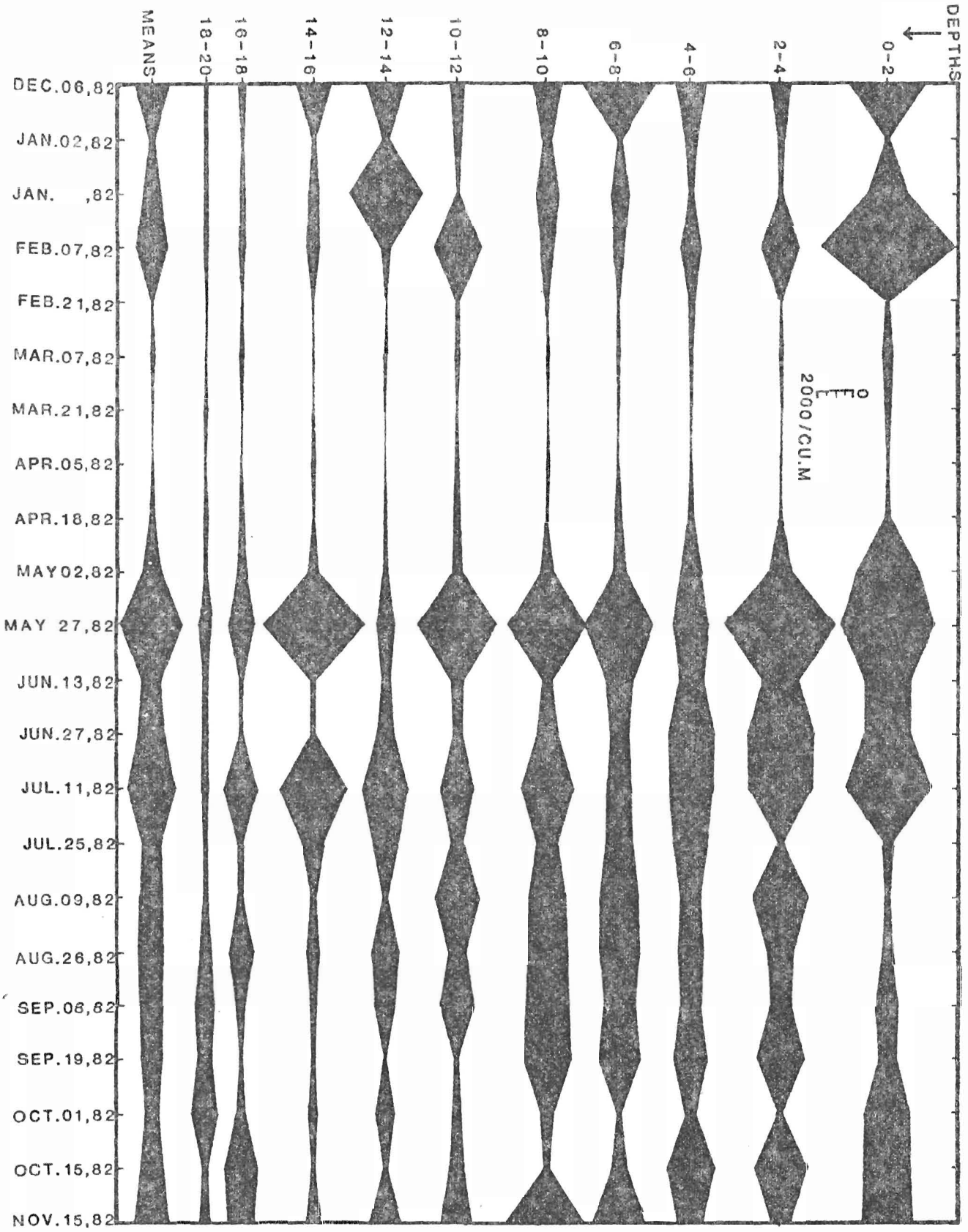
Daphnia pulex attained its maximum mean abundance in late May with four smaller peaks in February, July, November, and December (Fig.9). A minimum mean population size was observed in late March. Its population was low during the winter months.

Daphnia pulex was found at only a minimum population size of 14 $ind.m^{-3}$ in early April at 0-2 meters (Fig.9). However, 7,390 $ind.m^{-3}$ of this species were present at 0-2 meter in early February. Its populations were low during late winter and early spring. Three smaller peaks were observed in May, July and December. Population size of D. pulex were fairly high during summer and fall. Population of D. pulex showed gradual decrease with increasing depths. During the winter months its populations showed a rapid decline just below 2 meters. Whereas during the summer months population declines with depth were more gradual. On 7 sampling dates during winter and summer, D. pulex showed its maximum abundance at the chemocline. Though fewer in number, D. pulex was also present below the chemocline (Fig.9).

ii) Daphnia rosea

The abundance of Daphnia rosea reached a peak in summer and remained high during the fall and early winter (Fig.10). During late winter and early spring its population dropped to its lowest levels.

Figure 9. Vertical and temporal mid-day distribution of *Daphnia pulex* in Crawford Lake (depths in meters).


DEPTHS
0-2
2-4
4-6
6-8
8-10
10-12
12-14
14-16
16-18
18-20
MEANS
2000/CU.M
DEC.06,82
JAN.02,82
JAN. ,82
FEB.07,82
FEB.21,82
MAR.07,82
MAR.21,82
APR.05,82
APR.18,82
MAY02,82
MAY 27,82
JUN.13,82
JUN.27,82
JUL.11,82
JUL.25,82
AUG.09,82
AUG.26,82
SEP.06,82
SEP.19,82
OCT.01,82
OCT.15,82
NOV.15,82

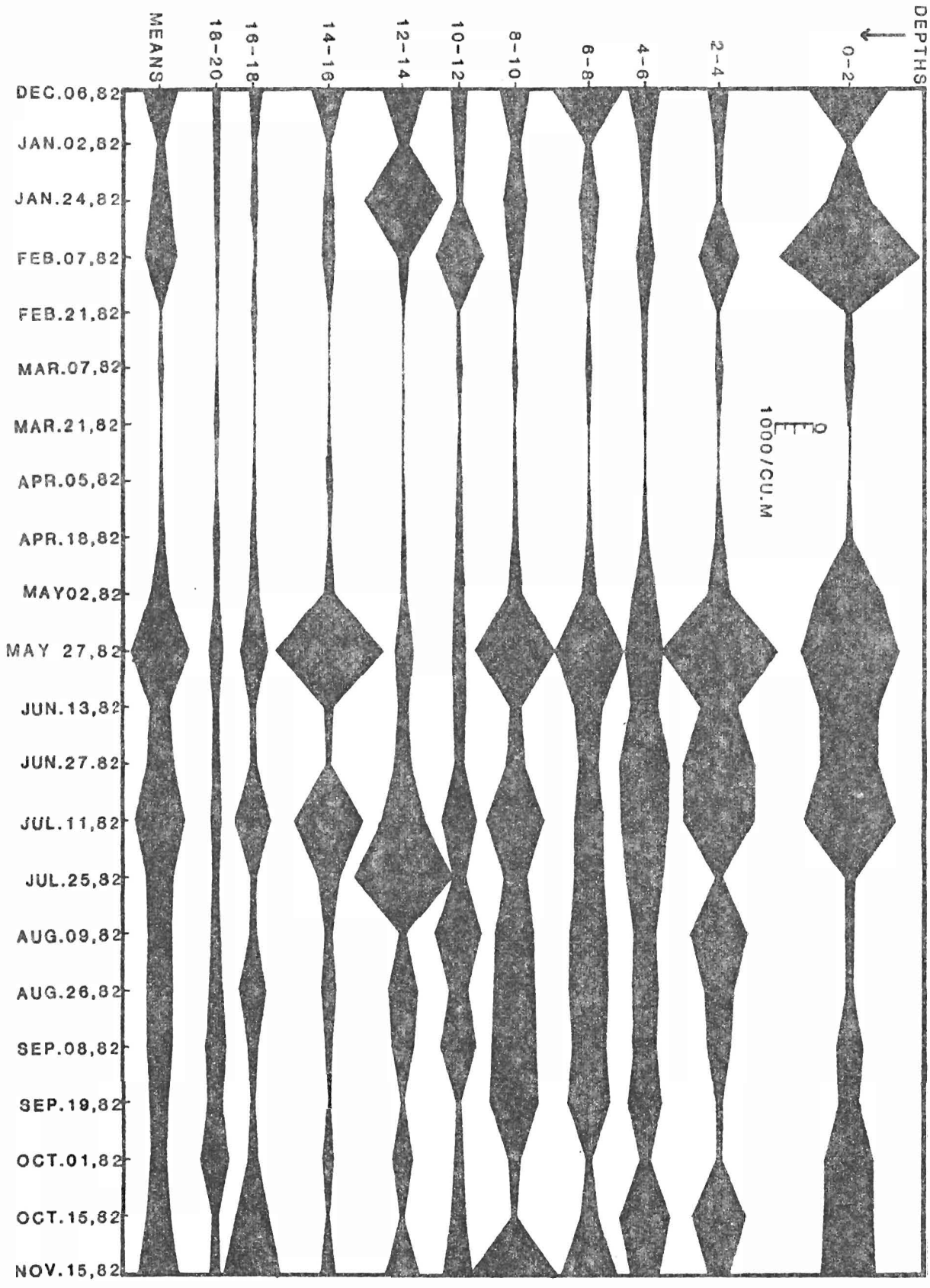
In the surface water (0-2m) D. rosea reached a maximum in the early winter and declined rapidly in March. Its population remained low during late winter and early spring. Late summer populations of D. rosea were low, and increased in early fall. Subsurface populations (below 4 meters) showed considerable decline with increasing depth during the entire period of investigation, but it was more rapid during the winter months. D. rosea was present in the anoxic monimolimnion on all sampling dates except in late February and early March (Fig.10). A maximum monimolimnetic population of 922 ind.m^{-3} was observed in early July.

The chemocline populations of D. rosea showed maximum abundance of 2,794 ind.m^{-3} in late May. By late March none were present (Fig.10). On some sampling dates (Feb.7, Apr.5, May 2 & 27, Jul.11, Aug.9, Sep.9, and Oct.15) their abundance at the chemocline was higher than in the immediately overlying waters (Fig.10). The reasons for this are discussed later.

iii) Survival of Daphnia in the anoxic monimolimnion

On June 09, 1983, three experimental tests were carried out to measure the optimum survival time of Daphnia in the anoxic monimolimnion (16-20m). For this purpose, Daphnia collected from the anoxic monimolimnion were kept in captivity at the chemocline. It was found that 50% of the single net tow organisms died in 20 to 25 minutes and the rest died within the next 75 minutes.

Figure 10. Vertical and temporal mid-day distribution of *Daphnia rosea* in Crawford Lake (depths in meters).


DEPTHS
MEANS
18-20
16-18
14-16
12-14
10-12
8-10
6-8
4-6
2-4
0-2
DEC.06,82
JAN.02,82
JAN.24,82
FEB.07,82
FEB.21,82
MAR.07,82
MAR.21,82
APR.05,82
APR.18,82
MAY02,82
MAY 27,82
JUN.13,82
JUN.27.82
JUL.11,82
JUL.25,82
AUG.09,82
AUG.26,82
SEP.08,82
SEP.19,82
OCT.01,82
OCT.15,82
NOV.15,82
1000/CU.M

iv) Distribution of pink and pale Daphnia

During the entire sampling period it was noticed that no pale Daphnia (body color transparent or other than pink or red) were found above 4-6 meters. The percentage of pink Daphnia increased below 6 meters with increasing depth and decreasing oxygen concentrations. The vertical distribution of pink and pale Daphnia on a single sampling date are shown in Table 3. Moreover, pale Daphnia were not found in the anoxic waters. A similar condition was noted from Crawford Lake by Prepas and Rigler (1978). However, they reported that no red (pink) Daphnia were found above 8 meters. They also reported that between 11 and 12 meters pink Daphnia suddenly increased from 5% to 100%. My investigation indicated that the per cent increase of pink Daphnia was more gradual. However, below 14 meters pink Daphnia represented 100% of the population (Table 3). This phenomenon was attributrd to the fact that Daphnia lose their haemoglobin from their body fluids in well aerated water and gain it in water containing low dissolved (Fox 1948)

v) Keratella quadrata

The population mean of Keratella quadrata reached its maximum during summer, declined in early fall and increased again in late fall (Fig.11). During winter the population declined and remained low until early May. A maximum abundance of 5,267 ind.m^{-3} was observed in late August. However, at the surface (0-2m), its population peaked in February, and again in May. Increases in abundance with increasing

Table 3. Vertical mid-day distribution of pale and pink *Daphnia* in Crawford Lake on June 9, 1983 and comparison with the results of Prepas and Rigler (1978).

Depths in meters	*pale *Daphnia	*Pink *Daphnia	*% of pink *Daphnia* in the total catch	*% of pink *Daphnia* from *Prepas and Rigler(1978).
0-2	135	o	0	0
2-4	70	0	0	0
4-6	36	1	3	0
6-8	80	20	20	5
8-10	145	250	63	100
10-12	12	120	91	"
12-14	8	90	92	"
14-16	0	150	100	"
16-18	0	38	"	"
18-20	0	14	"	"

depth were also observed in the summer months. The abundance maxima moved downward during summer and by July they were at their highest density at 12 meters. During the winter of 82, the population of K. quadrata was again highest in the surface waters (0-4m), and dropped rapidly just below 4 meters (Fig.11).

Below 12 meters, K. quadrata declined rapidly and remained at low and fairly low density throughout the monimolimnion. The chemocline populations were low during the entire period of investigation except in early January, May, June, and early September. At 16-18 meters depth a high abundance was observed on January 24.

vi) Keratella cochlearis

Keratella cochlearis reached a peak in abundance in December and decreased gradually thereafter (Fig.12). Three smaller peaks were observed in late spring, early and late fall (Fig.12). The mid summer populations were very low. The maximum and minimum mean population size was 72,094 ind.m^{-3} (December) and 76 ind.m^{-3} in July. During the winter months K. cochlearis was abundant in the upper mixolimnetic waters (0-6 m) and decreased rapidly below 6 meters. At the surface (0-2m) K. cochlearis reached its highest abundance in late January with smaller peaks in mid winter, early and late summer and late fall.

Aggregations of K. cochlearis at the chemocline were observed in December, January, and September. Monimolimnetic populations were also low except on those three sampling dates (Fig.12).

Figure 11. Vertical and temporal mid-day distribution of *Keratella quadrata* in Crawford Lake (depths in meters).

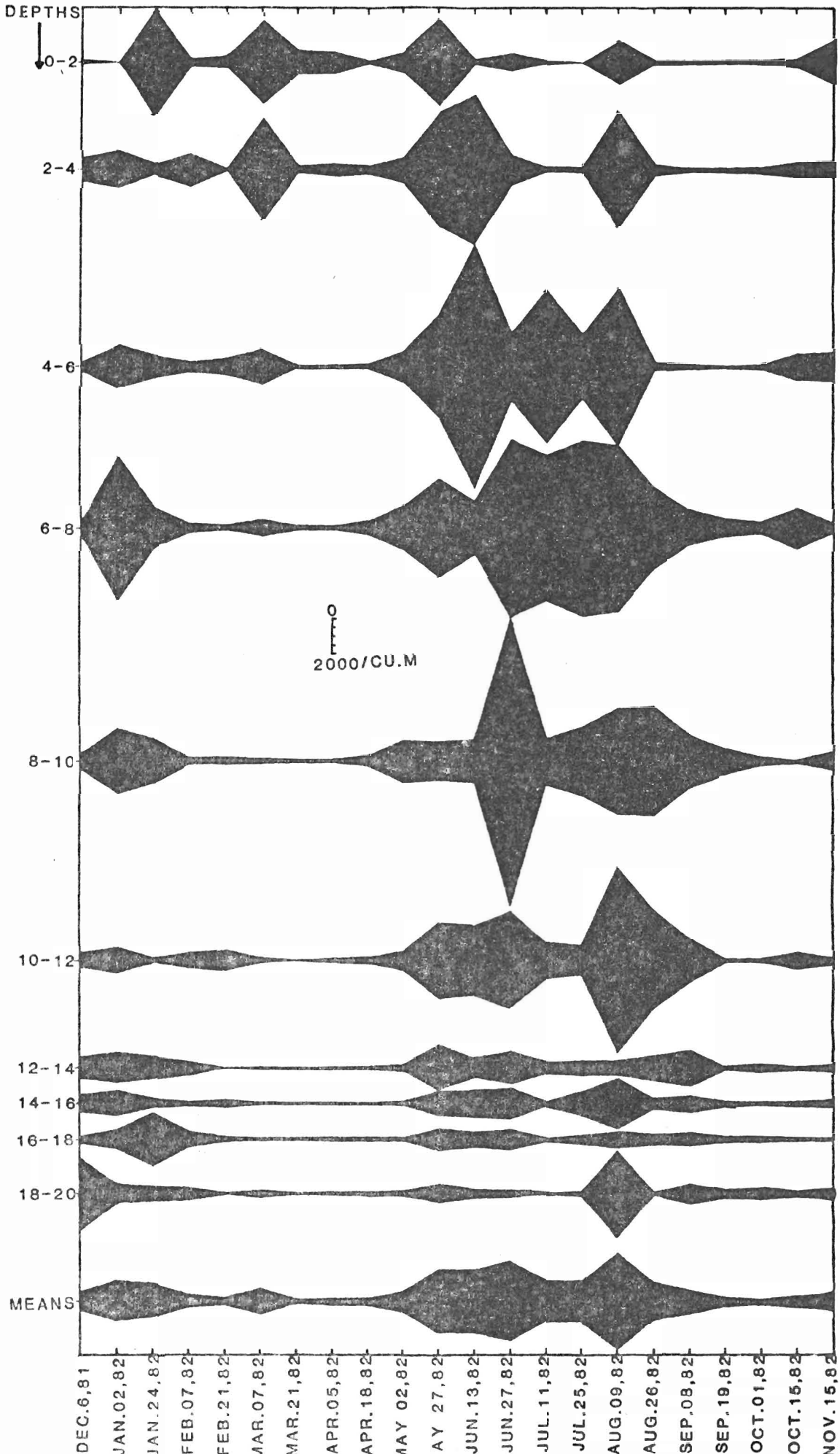
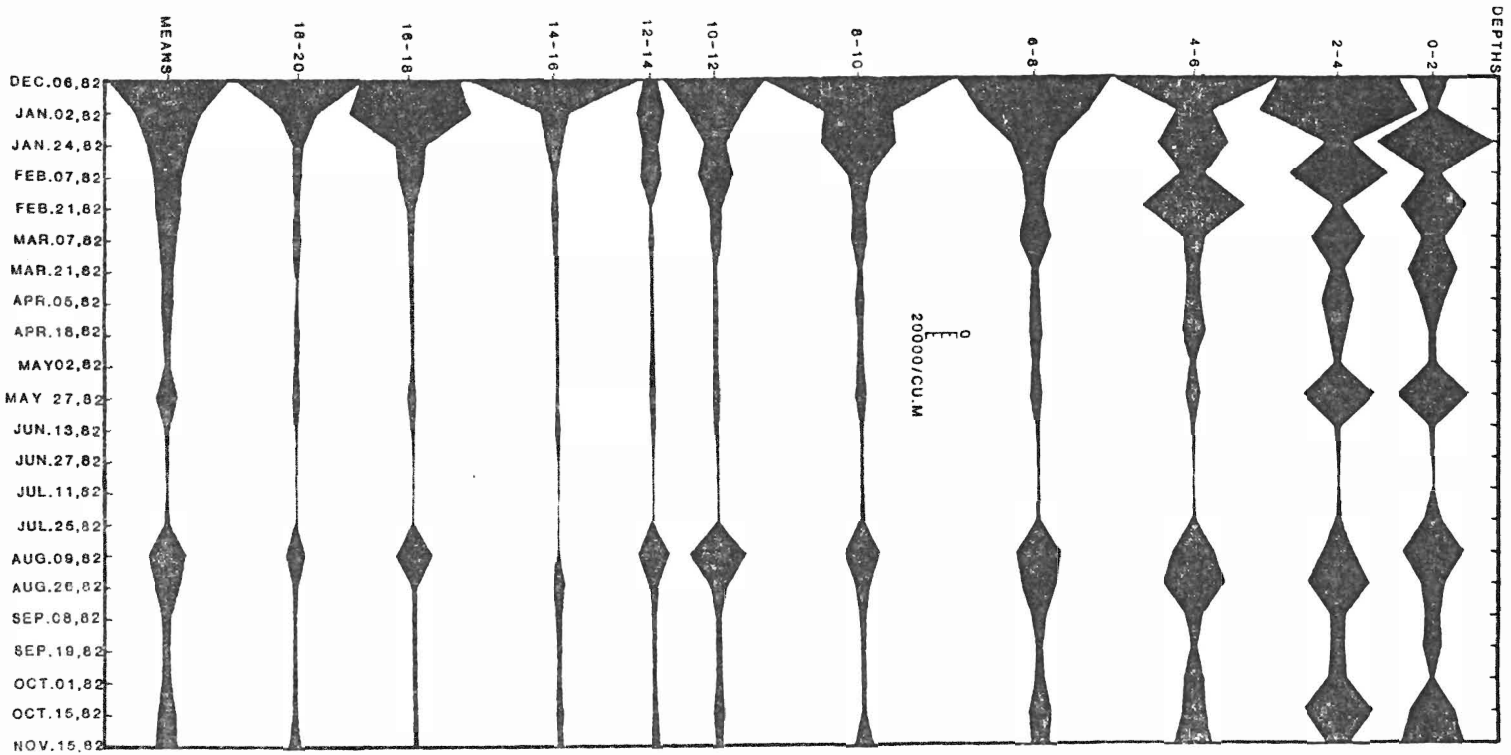

DEPTHS
0-2
2-4
4-6
6-8
8-10
10-12
12-14
14-16
16-18
18-20
MEANS
0
2000/CU.M
DEC.6,81
JAN.02,82
JAN.24,82
FEB.07,82
FEB.21,82
MAR.07,82
MAR.21,82
APR.05,82
APR.18,82
MAY 02,82
MAY 27,82
JUN.13,82
JUN.27,82
JUL.11,82
JUL.25,82
AUG.09,82
AUG.26,82
SEP.08,82
SEP.19,82
OCT.01,82
OCT.15,82
NOV.15,82

Figure 12. Vertical and temporal mid-day distribution of Keratella cochlearis in Crawford Lake (depths in meters).

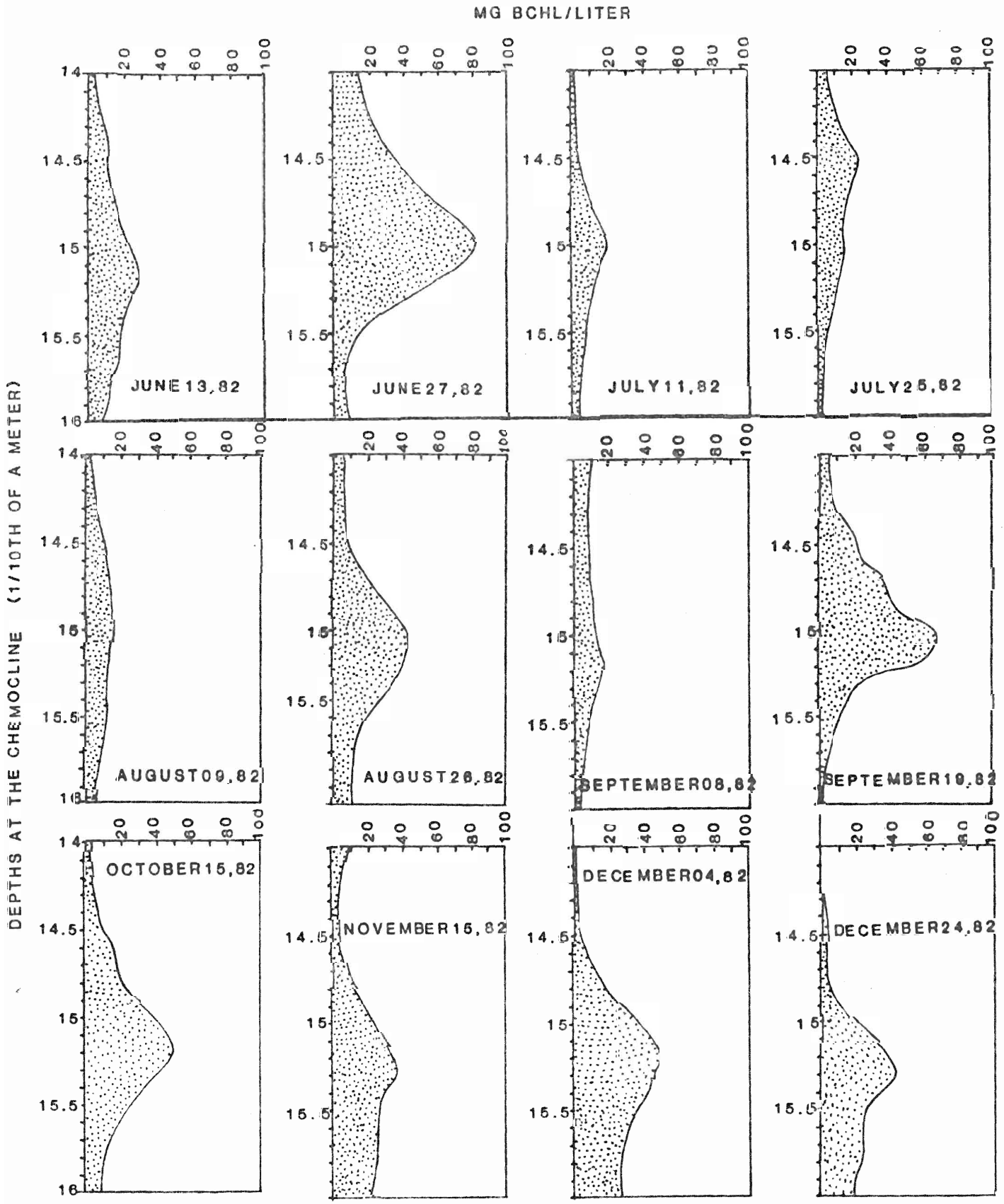

DEPTHS
0-2
2-4
4-6
6-8
8-10
10-12
12-14
14-16
16-18
18-20
MEANS
0
20000/CU.M
DEC.06,82
JAN.02,82
JAN.24,82
FEB.07,82
FEB.21,82
MAR.07,82
MAR.21,82
APR.05,82
APR.18,82
MAY02,82
MAY 27,82
JUN.13,82
JUN.27,82
JUL.11,82
JUL.25,82
AUG.09,82
AUG.26,82
SEP.08,82
SEP.19,82
OCT.01,82
OCT.15,82
NOV.15,82

C. TEMPORAL AND SPATIAL DISTRIBUTION OF PHOTOSYNTHETIC BACTERIA

Changes in the population size of photosynthetic bacteria with depth in different months were estimated by comparing the absorption spectra of acetone extracts of bacteriochlorophyll from water collected from selected chemocline depths (Fig.13). The temporal and spatial distribution of photosynthetic bacteria in mg $Bchl.l^{-1}$ was estimated only during the period of June,1982 to December,1982. Bacteriochlorophyll concentration was low (30 mg $Bchl.l^{-1}$) in early June. Maximal concentration of 81 mg $Bchl.l^{-1}$ was observed in late June and declined to 21 mg $Bchl.l^{-1}$ in early July. Later in summer the concentration increased to 42 mg $Bchl.l^{-1}$ with a further increase to 60 mg $Bchl.l^{-1}$ in late September. In October, bacteriochlorophyll concentration declined again to 22 mg $Bchl.l^{-1}$ and increased again in early December.

The vertical distribution of photosynthetic bacteria at the chemocline (14-16m) showed a sharp increase with depth and attained a peak density at a depth of 15 meters (Fig.13). The precise depths of these peak densities differed on different sampling dates shifting from 14.5 to 15.3 meters. In early June the maximum concentration was at 15.2 meters and moved up to 15.0 meters by late June. This peak concentration remained at 15.0 meters until mid July. In late July the bacterial population moved up and their peak densities observed at 14.5 meters. Later, the peak concentrations shifted down rapidly to 14.9 meters in early August and gradually to 15.1 and 15.2 meters in

Figure 13. Temporal changes in the vertical distribution of photosynthetic bacteria in Crawford Lake.


MG BCHL/LITER
DEPTHS AT THE CHEMOCLINE (1/10TH OF A METER)
JUNE13,82
JUNE27,82
JULY11,82
JULY25,82
AUGUST09,82
AUGUST26,82
SEPTEMBER08,82
SEPTEMBER19,82
OCTOBER15,82
NOVEMBER15,82
DECEMBER04,82
DECEMBER24,82

late August and early September. Except for late September, it remained at 15.2 meters depth with a slight shift to 15.3 meters in November, and late December.

D. ZOOPLANKTON AND PHOTOSYNTHETIC BACTERIA

Feeding experiments of zooplankton on photosynthetic bacteria were carried out five times in the summer and fall of 1982. By measuring the incorporation of ^{14}C-labelled photosynthetic bacteria as a function of time (0-16 minutes), it was demonstrated that for both Daphnia pulex and D. rosea the linear increase in radioactivity stopped within a range of 7-9 minutes (Figs.14-15). These time periods were used to calculate the ingestion and clearance rates of both species of Daphnia for different cell concentrations of food. Food concentrations, gut-passage times, radioactivity of individual zooplankton and single bacterial cell, ingestion and clearance rates are described and the data presented in Table 4. The concentration of labelled photosynthetic bacteria ranged from 1.4×10^{6} cells.ml^{-1} in August to 9.7×10^{6} cells.ml^{-1} on June 27. The ingestion rates of Daphnia pulex ranged from 8.3×10^{5} cells.ind.$^{-1}$ hr^{-1} on June 13 to 14.6×10^{5} cells.ind.$^{-1}$ hr^{-1}. Clearance rates ranged from 0.091ml.ind.$^{-1}$ hr^{-1} on June 27 to 1.000ml.ind.$^{-1}$ hr^{-1} on August 9. Daphnia rosea showed lower ingestion and clearance rates than D. pulex on all dates except July 25 (Table-1). Ingestion and clearance rates of D. rosea varied from 8.1×10^{5} on June 13 to 13.9×10^{5} cells.ind.$^{-1}$ hr^{-1} on

Figure 14. The uptake rate of radioactive 14C-labelled photosynthetic bacteria by Daphnia pulex. Vertical bars on July 25 analyses represent 95% confidence limits (n=3).

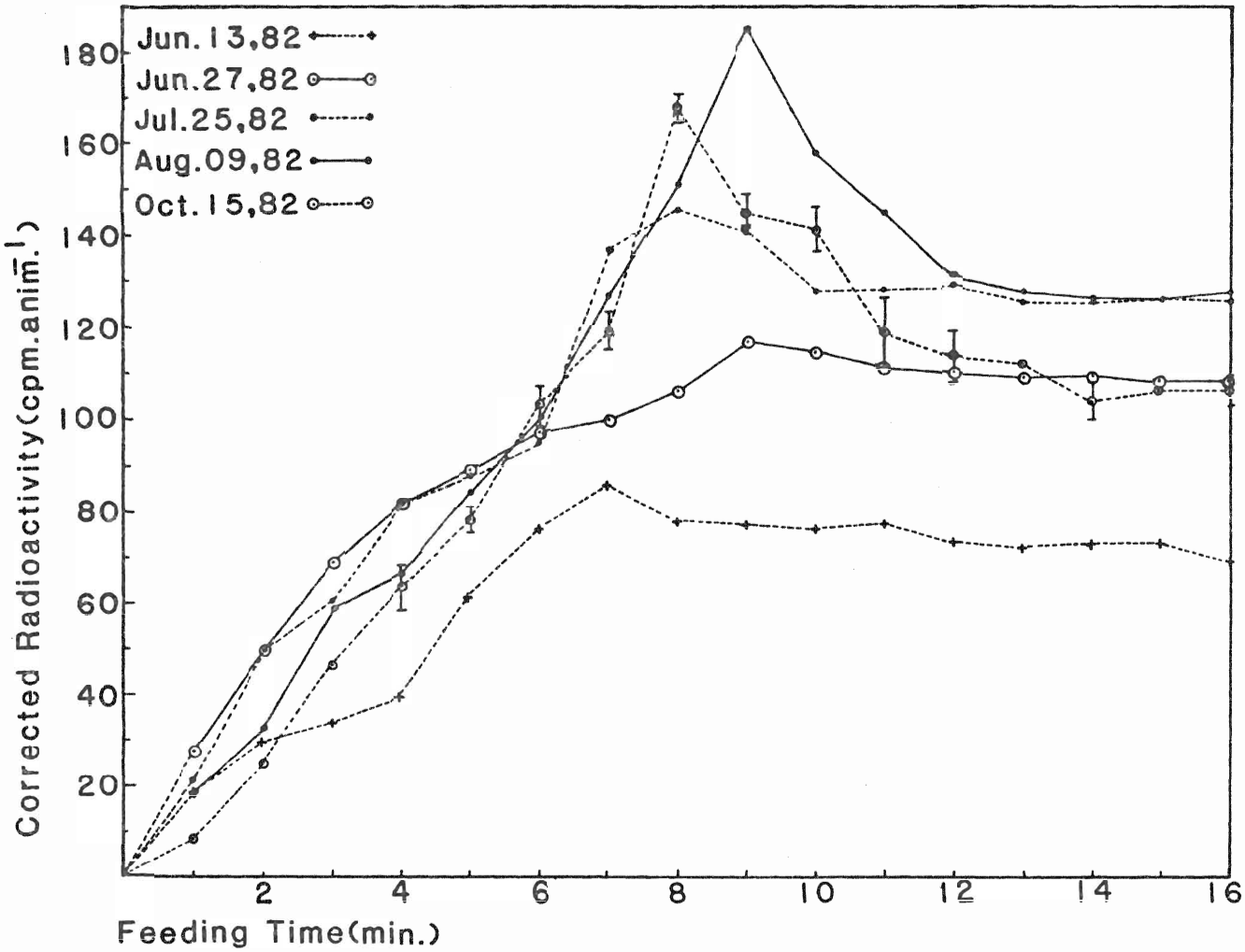

Jun.13,82
Jun.27,82
Jul.25,82
Aug.09,82
Oct.15,82
Corrected Radioactivity(cpm.anim.⁻¹)
180
160
140
120
100
80
60
40
20
2
4
6
8
10
12
14
16
Feeding Time(min.)

Figure 15. the uptake rate of radioactive 14C-labelled photosynthetic bacetria by Daphnia rosea. Vertical bars on July 25 analyses represent 95% confidence limits (n=3).

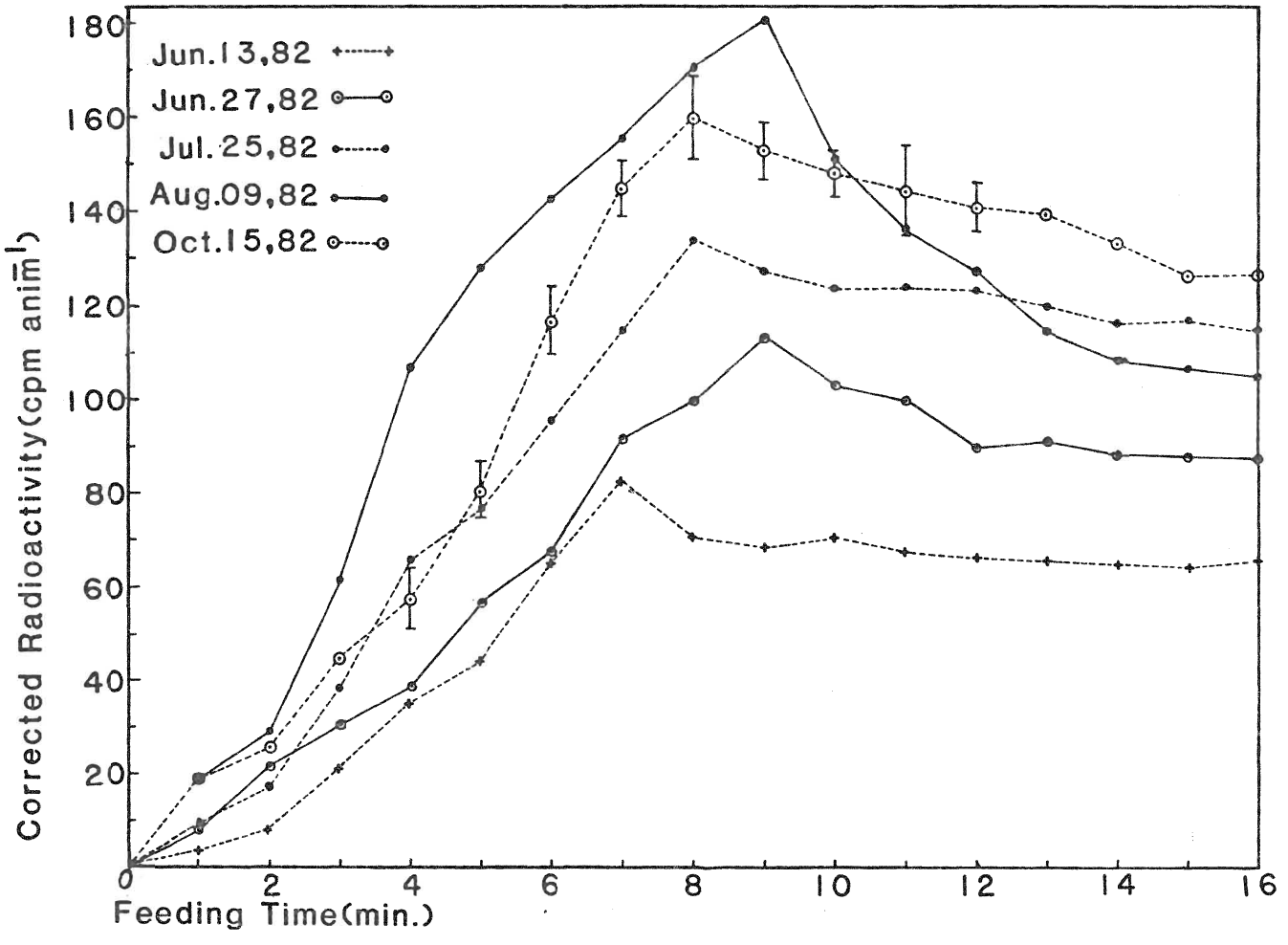

Jun.13,82
Jun.27,82
Jul.25,82
Aug.09,82
Oct.15,82
Corrected Radioactivity(cpm anim⁻¹)
Feeding Time(min.)
0
2
4
6
8
10
12
14
16
20
40
60
80
100
120
140
160
180

Table 4. Ingestion and clearance rates of Daphnia pulex and D. rosea on ^{14}C-labelled photosynthetic bacteria.

DATES ↓	CONCENTRATIONS OF BACTERIAL CELLS (#/ml)	INCUBATION TIMES (MINUTES)		RADIOACTIVITY/ANIM. (CPM/IND.ANIM.)		RADIOACTIVITY/CELL (CPM/CELL)	INGESTION RATES (CELLS/IND/HR)		CLEARANCE RATES (ML/IND/HR)	
		D. PULEX	D. ROSEA	D. PULEX	D. ROSEA		D. PULEX	D. ROSEA	D. PULEX	D. ROSEA
JUN. 13	2.1×10^6	7	7	85.5	83.0	0.00083	8.3×10^5	8.1×10^5	0.397	0.384
JUN. 27	9.7×10^6	9	9	117.0	113.8	0.00088	8.8×10^5	8.6×10^5	0.091	0.089
JUL. 25	1.9×10^6	8	7	146.0	134.0	0.0087	12.0×10^5	13.0×10^5	0.662	0.695
AUG. 09	1.4×10^6	9	9	185.0	181.0	0.00088	14.0×10^5	13.0×10^5	1.000	0.929
OCT. 15	1.6×10^6	8	8	168.0	160.0	0.00085	14.6×10^5	13.9×10^5	0.916	0.869
KERATELLA SP. ON AUG. 09		6		0.79			593		0.42 MICRO LITERS	

October 15 and 0.089 on June 27 to 0.929ml.ind.hr^{-1} $^{-1}$ on August 9 respectively.

Feeding of Keratella sp. on photosynthetic bacteria was carried out only once (August 9). Ingestion and clearance rates were 599 cells.ind.hr^{-1} $^{-1}$ and 0.42 micro liter.ind.hr^{-1} $^{-1}$ respectively.

The temporal and vertical distribution of the dominant zooplankton & photosynthetic bacteria, and the results of the ^{14}C labelled photosynthetic bacteria uptake experiments in Crawford Lake are described in the following section.

DISCUSSION

A. TEMPORAL AND SPATIAL DISTRIBUTION OF ZOOPLANKTON

Following ice-out at the end of April when the water temperatures increased abruptly (Fig.2), Daphnia and Keratella populations increased rapidly(Figs.9-12). Another zooplankton pulse was observed in early August following the algal bloom in late July. A similar seasonal pattern of zooplankton was reported by Northcote and Halsey (1969) in four meromictic lakes in British Columbia and Culver and Brunskill (1969) in the meromictic Fayetteville Green Lake. Abundance of all zooplankton species except K. cochlearis was low during winter.

The seasonal fluctuations of zooplankton were strongly related to temperature (Edmondson 1965; George and Fernando 1969). Edmondson and Litt (1982) mentioned that some increases in the size of the zooplankton population coincided with or came shortly after peaks in the abundance of food organisms. In the present study the higher abundance of K. cochlearis in winter was probably due to less predation and abundance of microflagellates, preferred food organisms which were particularly suitable for them (Dickman and Severn in press).

Both Daphnia pulex and D. rosea exhibited high abundance at the surface layers in the early winter,spring,and early summer and low abundance in late summer (Figs.9-10). Wetzel (1975) mentioned that some Daphnia exhibit maxima at the surface waters only during colder periods in spring and in the colder hypolimnion and metalimnion during summer stratification. This abundance of zooplankton in the deeper water

during summer stratification is most probably associated with heavy summer predation near the surface. All 4 zooplankton species especially K. quadrata were abundant at 8 to 11m in summer (Figs.9-12). The evidence for this is based on my observation that dissolved oxygen supersaturation associated with phytoplankton maxima moved downward from 5 meters to 11 meters (Fig.4). In addition, as the depth of the thermocline moved downward during summer (Fig.2), the phytoplankton population abundance as inferred from dissolved oxygen supersaturation also moved down.

B. CHEMOCLINE AGGREGATIONS

On the some of the sampling dates, D. pulex and D. rosea were higher in abundance at the chemocline than in the 12 to 14 meter overlying layer (Figs.9-10). K. quadrata also exhibited similar adundance at the chemocline (Fig.11), whereas K. cochlearis did not show such a substantial aggregation at that depth (Fig.12). Such an accumulation or aggregation of cladocerans and rotifers at the chemocline of meromictic lakes has been reported by several authors (Culver and Brunskill 1969; Sorokin 1969; Takahashi and Ichimura 1969; Larsson 1971; Guerrero et al 1978; Matsuyama and Shirouzu 1978). Northcote and Halsey (1969) reported that all zooplankton except Brachionus calyciflorus in Mahony and Lyons Lakes in British Columbia were restricted to the upper mixolimnion. A similar report has been published by Swift and Hammer (1979). They mentioned that most Daphnia

were found above 5 meters. Sorokin (1970) has provided evidence that this aggregation of zooplankton at the chemocline was stimulated by the availability of food for these organisms sush as photosynthetic bacteria. The same reason has been reported by others (Takahashi and Ichimura 1968; Matsuyama and Shirouzu 1978).

C. MONIMOLIMNETIC POPULATION OF ZOOPLANKTON

All four species of zooplankton were found in the anoxic monimolimnion (16-20m; Figs.9-12). Several previous reports indicated that a very few zooplankton were present in this layer, however, they also mentioned that those few found were dead or moribund (Northcote and Halsey 1969; Swift and Hammer 1979). Others reported fairly abundant populations in the anoxic monimolimnion (Culver and Brunskill 1969; Goehle and Storr 1978; Matsuyama and Shirouzu 1978). During the present investigation on Crawford Lake, zooplankton taken from the anoxic monimolimnion were alive and found to swim actively. However, their abundance in the monimolimnion was very low. This occurence of zooplankton in the anaerobic water created a complex situation because initially it was impossible to explain their presence and moreover, their survival in that layer. To make sure that those zooplankton were in fact living there, I collected several samples from the anaerobic layer by using differnt type of instruments such as a Brige-Juday closing net, a Schindler-Patalas sampler, a Van Dorn, and a Pump sampler. Both Closing net and Schindler-Patalas sampler showed approximately the same abundance whereas the Van Dorn and Pump samplers

showed no zooplankton. Finally to be absolutely sure about their occurance at that depth a plankton net was pulled horizontally through the bacterial plate for 3 meters with the help of a SCUBA diver (Dr. M. Dickman). The result of this tow showed an approximate similarity with the Brige-Juday closing net and Schindler-Patalas samples. It was concluded that the 6.8 liter Van Dorn and the 12 volt Pump sampler fail to accurately represent the natural zooplankton population at low population densities.

Rotifers were also found in the monimolimnion, but it was not known for how long they could survive in anoxic waters. From these observations it is believed that Daphnia do not stay in the monimolimnion (16-20m) for more than 20 to 25 minutes. It is predicted that they dive down to the monomolimnion and swim up again to the aerobic water before their haemoglobin stored oxygen (Prepas and Rigler 1978) is consumed. Usuki and Yamaguchi (1979) reported that when the dissolved oxygen concentrations was only 5% saturated, all pale Daphnia died in 3 hours, whereas pink individuals continued to swim normally in water with the same concentration at least for a day. However, there is no report available about their survival in water without dissolved oxygen. Rotifers were also found in the monimolimnion, but it was not known for how long they could survive in anoxic waters.

D. TEMPORAL AND SPATIAL DISTRIBUTION OF PHOTOSYNTHETIC BACTERIA

The chemocline of meromictic lakes provides the necessary H_2S and

CO_2 to the photosynthetic bacteria there (Northcote and Halsey 1969). In Crawford Lake, water collected from the chemocline was pinkish in color. It was found by SCUBA diving that the photosynthetic bacteria formed a 2 meter thick cloud on June 11,1983. Hamner et al (1982) reported a 3 meter thick photosynthetic bacterial plate in a meromictic lake in Palau.

Analysis of the water from the bacterial plate during summer and fall months was performed using a spectrophotometer as described in the methods section. A maximum density of 81 mg $Bchl.l^{-1}$ was recorded in Crawford Lake. Two maxima one in late June and another in late September occurred (Figs.13-16). A smaller peak in the photosynthetic bacterial density was observed in late August. The present estimates of bacteriochlorophyll concentrations (14 to 81 mg $Bchl.l^{-1}$) were higher than those reported from Japanese lakes (6 to 18 mg $Bchl.l^{-1}$; Takahashi and Ichimura 1968). Severn (1982) reported a maximum concentration of 24 mg $Bchl.l^{-1}$.

Steenbergen and Korthals (1982) mentioned that light intensity and sulfide concentrations limited the position of photosynthetic bacteria in Lake Vechten. In meromictic Faytteville Green Lake, photosynthetic bacteria were found to be limited by light only during the snow and ice cover period (Culver and Brunskill 1969). Light intensities reaching the bacterial layer in Crawford Lake were very low and ranged from 0.002 to 3.00 $\mu En.m^{-2}.s^{-1}$. In meromictic Knaack Lake, Parkin and Brock (1981b) reported that light intensities at 2.2m were in the range of 0.5 to 2.0 $\mu En.m^{-2}.s^{-1}$, however, at the depth where sulfide was present during the day (2.4m), light intensities were much lower (0.05 to 0.5

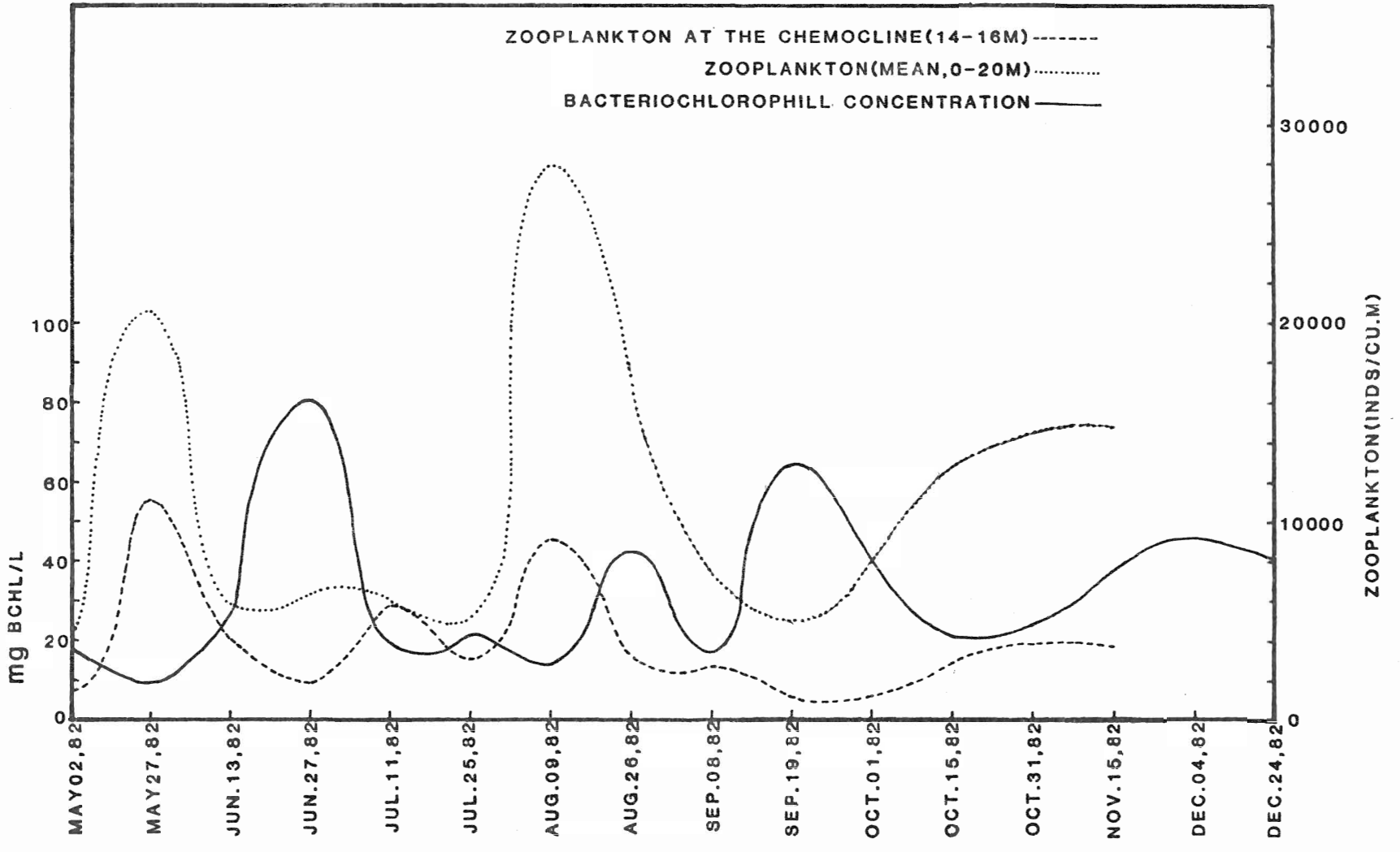
$\mu En.m^{-2}.s^{-1}$). They showed that the photosynthetic bacterial population in Knaack Lake was light limited at intensities less than 0.5 $\mu En.m^{-2}.s^{-1}$ but light intensities more than 0.5 $\mu En.m^{-2}.s^{-1}$ were saturating for photosynthesis. A comparison of Fig.13 and Table 1 demonstrated that the lower limit of photosynthetic bacteria at 16m was established by the light intensity. Light intensities below 16m in Crawford Lake were less than 0.05 $\mu En.m^{-2}.s^{-1}$ on all but 2 sampling occasions. Parkin and Brock (1981b) stated that below this light intensity photosynthetic bacteria failed to occur.

Although the light intensities reaching the bacterial layer in Crawford Lake were lower than the range reported from Knaack Lake, no limiting effect of low light intensity on the temporal fluctuations of bacterial population density were observed. The evidence for this was the inconsistent relationship between the temporal changes in light intensity at the bacterial layer and the bacterial population density. Severn (1982) reached the same conclusion.

E. PHOTOSYNTHETIC BACTERIA AND ZOOPLANKTON

In Crawford Lake, photosynthetic bacteria were found to demonstrate an inverse relation with the zooplankton population at the bacterial layer (Fig.16). Such as on June 27 and September 19 when zooplankton at the bacterial layer were very low, photosynthetic bacteria populations were high. Moreover, at high zooplankton densities

Figure 16. Temporal distribution of all 4 dominant zooplankton combined, for the chemocline & for the entire water column. Photosynthetic bacteria at the chemocline are represented as line.


ZOOPLANKTON AT THE CHEMOCLINE(14-16M)
ZOOPLANKTON(MEAN,0-20M)
BACTERIOCHLOROPHILL CONCENTRATION
mg BCHL/L
ZOOPLANKTON(INDS/CU.M)
0
20
40
60
80
100
0
10000
20000
30000
MAY02,82
MAY27,82
JUN.13,82
JUN.27,82
JUL.11,82
JUL.25,82
AUG.09,82
AUG.26,82
SEP.08,82
SEP.19,82
OCT.01,82
OCT.15,82
OCT.31,82
NOV.15,82
DEC.04,82
DEC.24,82

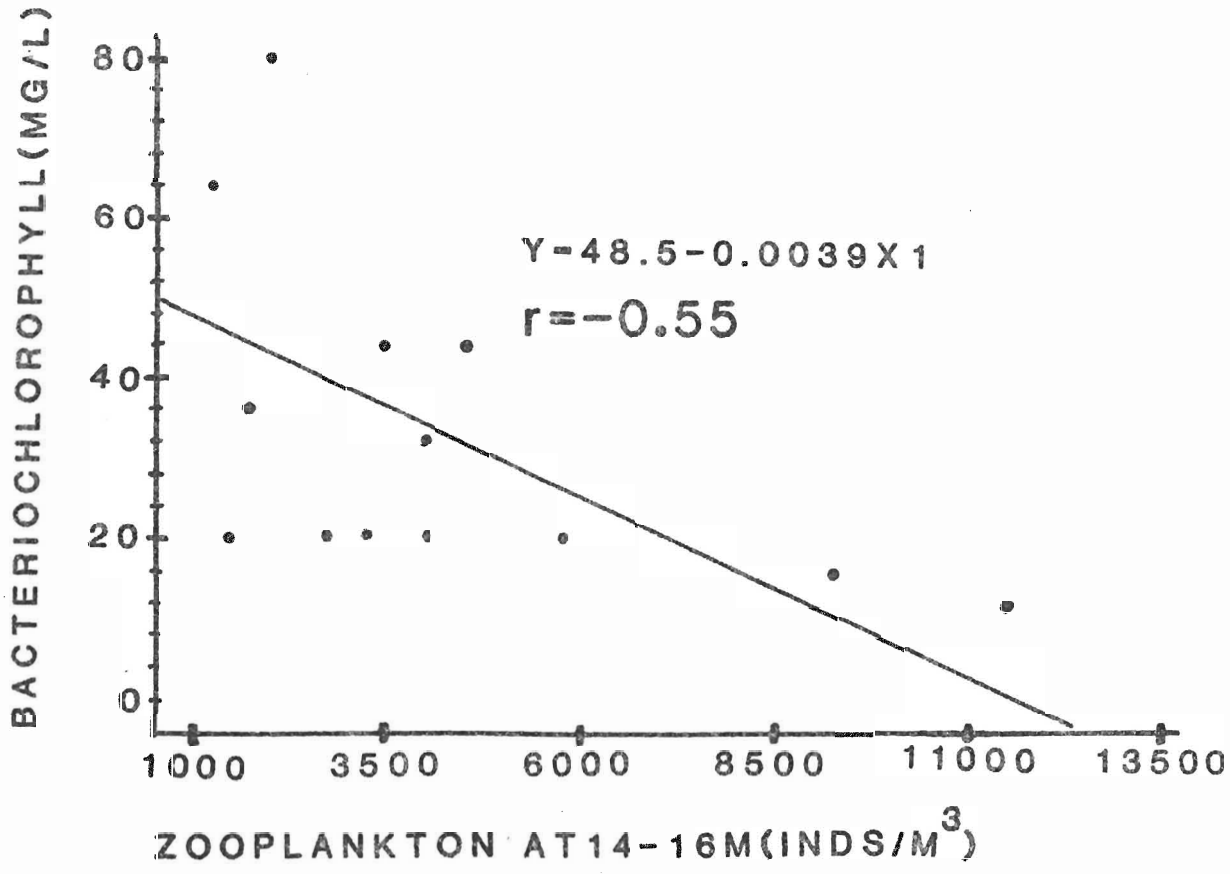
(May 27, July 11, and August 09), photosynthetic bacterial population was low (Fig.16). This negative correlation may possibly be due to a controlling effect of zooplankton grazing on photosynthetic bacteria (Fig 17). However, this relationship was not sufficient to conclude that zooplankton control the photosynthetic bacterial population in Crawford Lake. Guerrero et al (1978) mentioned that when the maximum number of zooplankton occurred in the water column of Lago Banolas a sharp reduction of the total bacterial population was observed. They concluded that this was probably due to zooplankton grazing.

F. TEMPORAL VARIATION IN THE DEPTH OF THE BACTERIAL PLATE

Although the location of the bacterial plate in meromictic lakes is well documented in the literature (Takahashi and Ichimura 1968; Culver and Brunskill 1969; Matsuyama and Shirouzu 1978; Hammer 1981; Hamner et al 1892; Steenbergen and Korthals 1982), temporal changes in the vertical position of the bacterial plate were only noted by Northcote and Halsey 1969, Dickman and Artuz 1978 & Parkin and Brock 1981a . In the present investigation, the depth of the maximum bacterial density was considered as the representative depth of the layer. A shift in that depth was taken to indicate its temporal changes (Fig.13). The same procedure was followed by others (Northcote and Halsey 1969; Parkin and Brock 1981a).

In Crawford Lake, the photosynthetic bacterial layer shifted from 14.5 meters on July 25 to 15.3 meters on December 24. The changes in the position of the bacterial layer demonstrated in this study (Fig.13)

Figure 17. Regression analysis of bacteriochlorophyll concentrations and zooplankton abundance at the chemocline (14-16m).


BACTERIOCHLOROPHYLL(MG/L)
80
60
40
20
0
Y=48.5-0.0039X1
r=-0.55
1000
3500
6000
8500
11000
13500
ZOOPLANKTON AT14-16M(INDS/M3)

may have been a response to changes in the depth of the O_2-H_2S boundary. In the summer, the position of the layer was at 15 meters which was at the depth of zero oxygen concentration. Following the algal bloom in late July as the O_2-H_2S boundary moved up to 14.5 meters, the bacterial layer also moved up to that depth. On the other hand, following the fall mixing in early December, the maximum bacterial density was observed at 15.3 meters. Northcote and Halsey (1969) reported a similar seasonal changes in the level of the photosynthetic bacterial layer in both Mahoney and Lyons Lakes. They mentioned that the position of the bacterial plate increased in depth as light penetration and the depth of the mixolimnion increased. In both lakes the layer dropped down from 8.0 meters in July to 9.2 meters in August. It was at 8.6 meters following the fall overturn in November. It can be suggested that in Crawford lake this shifting in the depth of the bacterial layer was influenced by two factors acting at different times of the year. Following the late spring and early summer algal bloom, decaying organic matter from the upper mixolimnion accumulated on or near the chemocline where its continued decomposition removed the dissolved oxygen from the overlying water mass (Figs.6-7). This process decreases the thickness of the aerobic mixolimnion. This in turn permits the photosynthetic bacteria to move up (Dickman and Artuz 1978). However, the bacterial layer in Crawford Lake did not move up to the top of the anaerobic layer because of the absence of H_2S above 14.5 meter. As the bacterial layer moved up to 14.5m the oxidation of sulfide to sulfate by the bacteria prevented their further upward migration. During fall mixing, deeper water in the lower mixolimnion and upper monimolimnion were mixed and intrusion of

oxygen into the previously anaerobic water resulted in the mass mortality of the photosynthetic bacteria (Dickman and Severn in press). It is also believed that photosynthetic bacteria at the newly established O_2-H_2S boundary grow faster and attain the peak density. The evidence for this is based on the higher density of the bacteria at the deeper layer (15.3m) on December 24 (Fig.13).

Parkin and Brock (1981a) reported that the photosynthetic bacteria reached their maximum densities at the depth where neither O_2 and H_2S were detected. Analyses by Dr. Harry Thode of McMaster University of H_2S concentrations at the chemocline indicated 1ppm that they increased to 9ppm below the chemocline in Crawford Lake. Dissolved oxygen was never detectable at the depth of maximum bacterial density.

In the preceding discussions, it has been mentioned that aggregations of zooplankton at the photosynthetic bacterial layer may be due to the presence of these bacteria as a food source for the zooplankton. In addition the pink coloration of the gut contents of *Daphnia* species suggests that they were feeding on the photosynthetic bacteria. Spectral analyses of the gut contents of *Daphnia* spp. in Crawford Lake (Severn 1982) demonstrated that they were consuming photosynthetic bacteria. Similar observations were made by several authors (Sorokin 1969; Goehle and Storr 1978; Swift and Hammer 1979). In the following discussion more direct evidence of zooplankton feeding on photosynthetic bacteria and their rates of feeding will be provided.

G. FEEDING OF ZOOPLANKTON ON PHOTOSYNTHETIC BACTERIA

In the present study, an "in situ" radioactive-tracer method was adopted to demonstrate the feeding of zooplankton on photosynthetic bacteria under natural conditions. Haney (1973b) suggested three problems inherent in this method: 1) the lack of assurance that all components of the food cells were equally labeled with ^{14}C, 2) the excessively long experimental period during which significant egestion may have occurred, and 3) the absence of other zooplankton and phytoplankton forms which may have influenced the filtering rates.

The first problem was eliminated in my study because only photosynthetic bacteria were available at the chemocline and their size ranges were minimal (0.8-1.4um in length and 0.7-0.9um in width; Severn 1979). The second problem listed above was resolved by using natural populations of zooplankton. The third problem was resolved by conducting separate feeding experimental runs for a time period of only 0 to 16 minutes. Egestion times for each species of Daphnia and Keratella sp. were recorded by plotting radioactive uptake per individual against feeding time.

During 5 experimental runs, the egestion time or gut-passage time of Daphnia pulex and D.rosea ranged from 7 to 9 minutes (Table 4). Although the egestion times for both species were within the same range, the radioactive uptake rates were always more for D. pulex than for D. rosea. This demonstrated that D. pulex had a higher filtering rate than D. rosea. This agrees well with the estimates of Burns and Rigler (1967) for Daphnia rosea (7 min.), and Matsuyama & Shirouzu

(1978) for Daphnia species (8 min). Slightly higher egestion times (10 min.) have been reported by Bogdan and McNaught (1975). While Haney (1973b) reported a shorter egestion time (5 min.) for D.rosea. A much lower range of egestion times (2-5 min.) was reported by Zankai (1983). He explained that due to the combined effects of the high concentrations of food relative to the gut filling time and high water temperatures (20-25 ^{o}C) during summer, the time necessary for the food to pass through the gut was shortened to 2-5 minutes. He also mentioned that gut-passage time or egestion time was influenced by the species, their size, the ambient temperature, and the amount of food.

The present experiment did not demonstrate any consistent relationship between egestion times, body size and food concentrations. Although D. pulex were larger (1.1-1.6mm) than D. rosea (0.8-1.2mm), their egestion times showed very little variations at similar food concentrations. Keratella sp. being much smaller than Daphnia exhibited a 6 min. egestion time. This was much longer than for Daphnia if expressed in terms of body size.

Temperatures at the chemocline remained approximately the same (4.8-5.7 ^{o}C) during the experimental period (Fig.2), and therefore no effect of temperature on egestion time was likely.

The in situ ingestion rates of D. pulex and D. rosea ranged from $8.3X10^{5}$ to $14.6X10^{5}$ cells.ind.$^{-1}$hr.$^{-1}$ and $8.1X10^{5}$ to $13.9X10^{5}$ cells.ind.$^{-1}$hr.$^{-1}$ respectively (Table 4). The single ingestion rate estimate for Keratella species (599 cells.ind.$^{-1}$hr.$^{-1}$) and a clearance rate of 0.42 µl.ind.$^{-1}$hr.$^{-1}$ was lower than for any of the crustaceans studied. The clearance rates of D. pulex and D. rosea ranged from 0.091 to

1.000 ml.ind.hr^{-1} ($\bar{X}$= 0.613 ml.ind.hr^{-1}) and 0.089 to 0.929 ml.ind.hr^{-1} ($\bar{X}$= 0.593 ml.ind.hr^{-1}) respectively.

It was very difficult to compare the present estimates with published data because of the differences in the size of the animals, size and concentration of food particles, water temperatures and the duration of the experiments. Starkweather et al (1979) reported clearance rates of 0.3 µl.ind.hr^{-1} for Brachionus calyciflorus feeding on bacteria. These agree well with the present estimates for the approximately similar sized Keratella species (Table 5). Haney (1973a) also noted a similar rate of 0.3 µl.ind.hr^{-1} for Kellicotia species feeding on yeast cells. Nauwerck (1959) reported the clearance rates between 0.1 and 1.2 µl.ind.hr^{-1} for a mixed population of rotifers. Keratella cochlearis was found to exhibit a clearance rate of 1.4 µl.ind.hr^{-1} in an eutrophic lake (Bogdan and Gilbert 1982) which was approximately 3 times higher than the present estimates. The range of clearance rates estimated for D.pulex and D. rosea during the present experiments were similar to several previous estimates on different Daphnia species (Haney 1973a; Bogdan and McNaught 1975; Zankai 1983). Filtering rates of Daphnia species estimated by Paterson et al (1978) on bacterial cells (0.20 to 1.50 ml.ind.hr^{-1}) were also similar to the present estimates whereas the rates on larger particles were much higher (Table 5).

Others reported 4-6 times higher filtering rates (Rigler 1961; McMahon and Rigler 1965) while some estimates were much lower than the present ones (Nauwerck 1959; Haney and Hall 1975; Gulati 1978; Bogdan and Gilbert 1982). It becomes apparent from Table 5 that filtering

Table 5. Clearance rates of cladocerans and rotifers in the present and previous studies.

Species	Size of animals (mm)	Food cells	Clearance rates (ml/ind/hr)	Authors
Daphnia pulex	1.1-1.6	photo-bacteria	0.091-1.000 $\bar{X}$=o.613	Present study
Daphnia rosea	0.8-1.2	"	0.089-0.929 $\bar{X}$=0.593	"
Keratella sp.	-	"	0.420µl	"
Daphnia cucullata	1.2-1.6	Chlorella	0.130-0.540 $\bar{X}$=0.325	Zankai (1983)
Daphnia hyalina	1.2-1.7	"	0.100-0.760 $\bar{X}$=0.430	"
Daphnia galeata	1.2-1.6	"	0.200-0.780 $\bar{X}$=0.380	"
Bosmina longispina	.36-.42	Chlamydomonas	3.20 µl	Bogdan & Gilbert (1982)
Keratella cochlearis	-	"	1.40 µl	"
Brachionus calyciflorus	-	bacteria + yeast	o.30 µl	Starkweather et al (1979)
Daphnia sp.	-	-	0.10-0.20	Gulati (1978)
Daphnia sp.	2.4	bacteria	0.20-1.50	Paterson et al (1978)
Daphnia sp	"	larger particles	2.00-6.00	"
Daphnia galeata	1.3	nannoplankton	0,13-0.46	Bogdan & McNaught (1975)
Daphnia galeata	1.4	-	0.04	Haney & Hall (1975)
Daphnia galeata	1.5-1.7	-	0.33	Haney (1973a)
Kellicotia sp.	-	-	0.3 µl	"

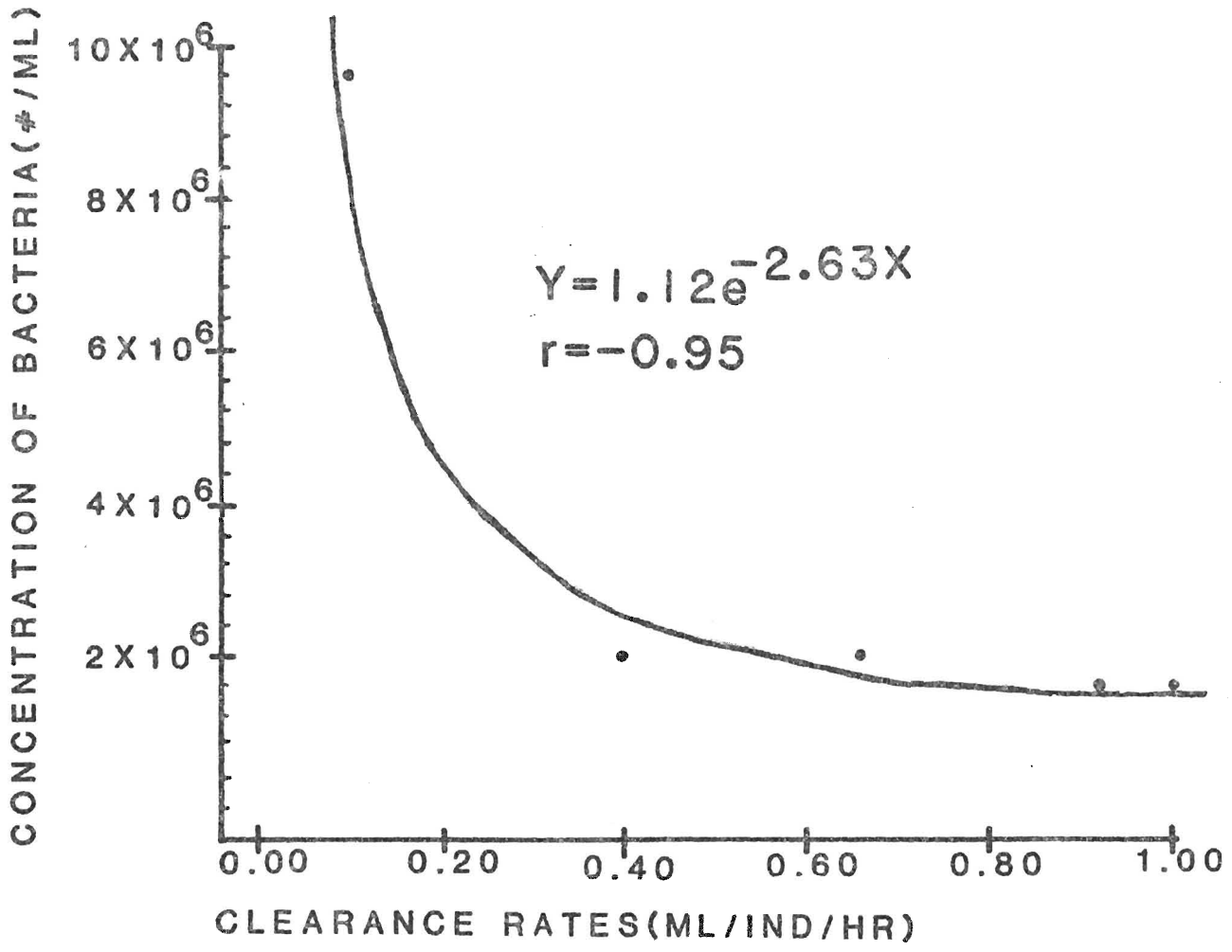
Table 5 (continued).

Species	Size of animals (mm)	Food cells	Clearance rates (ml/ind/hr)	Authors
Daphnia magna	-	*E. coli*	3.40	McMahon & Rigler (1965)
D. magna	-	*Chlorella*	2.70	"
Daphnia sp	-	Yeast	2.60	Rigler (1961)
Daphnia longispina	-	Phytoplankton	.008-0.190	Nauwerck (1959)

rates for a single zooplankton species are quite variable and are influenced by a number of critical factors. Gliwicz (1969) suggested that crustacean and rotifer filtering rates based on a collection of bacteria sized particles are with some exceptions, lower than those for larger foods. Estimates for zooplankton fed on bacteria and larger particles corraborates this point (Paterson et al 1978).

Except on one occasion (July 25), D. pulex exhibited higher ingestion and clearance rates than D. rosea (Table 4). The higher ingestion and clearance rates of D. pulex appear to match with its larger body size. Similar relationships have been reported by others (Burns and Rigler 1967; Burns 1968; Haney 1973a; Haney and Hall 1975; Hall et al 1975; Paterson et al 1978; Downing and Peters 1980; Bogdan and Gilbert 1982; Zankai 1983). During the present experiments, clearance rates of both species of Daphnia were found to be inversely related with bacterial densities (Table 4). The highest clearance rates were observed at the lowest bacterial densities (August 09). The reverse of this was found on June 27. In other words, clearance rates of Daphnia pulex demonstrated a strong dependence on the density of food cells (Fig. 18). As a similar exponential relation was found for D. rosea, it is not shown in the figure. Bogdan and Gilbert (1982) reported a similar inverse relationship for Bosmina and Keratella feeding on Clamydomonas. However, they mentioned that temperature was the primary environmental factor controlling the variations in clearance rates throughout the season, while the concentration of food particles was important in controlling the clearance rates at a constant temperature. During the present study, temperature was fairly

Figure 18. Exponential relationship between concentration of photosynthetic bacteria and clearance rates of Daphnia pulex.


CONCENTRATION OF BACTERIA(#/ML)
10X10^6
8X10^6
6X10^6
4X10^6
2X10^6
Y=1.12e^-2.63X
r=-0.95
0.00
0.20
0.40
0.60
0.80
1.00
CLEARANCE RATES(ML/IND/HR)

constant (4.8-5.7 °C). Thus Bogdan and Gibert's explanation of the effects of food concentrations at constant temperature agrees well with my observations. They also mentioned that they could not determine the regulatory mechanisms responsible for the inhibitory effects of high particle concentrations. Increased food concentrations may overload the feeding apparatus and cause filtering efficiency to decrease even though the behavior of the animals did not change (Bogdan and Gilbert 1982). Starkweather et al (1979) reported that ingestion rates are strongly density dependent, reaching maximal values at the highest food densities tested. The present observations differed from this report and ingestion rates did not demonstrate any consistent relation with food density, whereas it agrees with the relationship observed by Downing and Peters (1978).

H. IMPACT OF ZOOPLANKTON GRAZING ON PHOTOSYNTHETIC BACTERIA

As mentioned earlier in the introduction only two previous works (Sorokin 1969; Matsuyama and Shirouzu 1978) report on the feeding of zooplankton on photosynthetic bacteria, but those did not include the quantitative estimations of feeding rates. Therefore, data derived in this study would increase our understanding of the contribution of photosynthetic bacteria to the diet of the filter feeding zooplankton.

Considering the inverse relationship of zooplankton populations and photosynthetic bacterial densities as a natural condition prevailing in the lake (Figs.16-17), it appears that the edible

Table 6. Population ingestion and clearance rates of Daphnia pulex (D. p.), D. rosea (D.r.), Keratella spp.(K.sp) feeding on photosynthetic bacteria in Crawford Lake.

	Population density (ind.m^{-3})			Population clearance rates ($l.m^{-3}.day^{-1}$)			Population ingestion rates (cells.$m^{-3}.day^{-1}$)		
	D.p.	D.r.	K.sp.	D.p.	D.r.	K.sp	D.p.	D.r.	K.sp.
Jun.13	199	107	1364	1.90	0.99	-	3.9×10^{9}	2.1×10^{9}	-
Jun.27	135	78	750	0.30	0.17	-	2.8×10^{9}	1.6×10^{9}	-
Jul.25	748	353	525	11.88	5.89	-	2.3×10^{10}	1.1×10^{10}	-
Aug.09	234	117	7649	5.62	2.61	0.023	7.8×10^{10}	3.6×10^{10}	3.3×10^{10}
Oct.15	936	458	1278	20.58	9.55	-	3.3×10^{10}	1.5×10^{10}	-
Means	450	223	2321	8.05	3.84	-	1.4×10^{10}	9.3×10^{9}	-

photosynthetic bacteria are not able to grow faster than the loss caused by the population clearance rates of zooplankton in Crawford Lake (Table 6). As zooplankton population estimates and the *in situ* feeding experiments were carried out on the same day, it was possible to couple the zooplankton population density and the individual clearance rates to obtain the population clearance rates. However, it was assumed that the ingestion and clearance rates of zooplankton feeding on photosynthetic bacteria remained the same at different times of the day. The noon hour (10AM-2PM) estimates of filtering rates were used to estimate the population ingestion and clearance rates of zooplankton. I estimated that on the average, *Daphnia pulex*, *D. rosea*, and *Keratella* spp remove the particulate material from approximately 8.0, 3.4, and 0.023 liters of water per day respectively (Table 6).

The regeneration times of photosynthetic bacteria in Crawford Lake are a function of temperature (5-6^{o}C), light intensity (0.002-3 uEn.m.$^{-2}$s^{-1}), and H_2S concentrations (0.1-1.0 ppm, Thode 1983). On the basis of this it was possible to estimate the range of regeneration times of photosynthetic bacteria in Crawford Lake as 3-8 hours from the laboratory studies of Clayton and Systrom (1978).

The concentration of photosynthetic bacteria in Crawford Lake ranged from $1.4X10^6$ to $9.7X10^6$ cells.ml^{-1}. This range of bacterial density was multiplied by the range of bacterial regeneration times to estimate the daily production of photosynthetic bacteria. From the daily production of photosynthetic bacteria and the daily population clearance rates of *Daphnia pulex* and *D. rosea*, their per cent consumption of the total daily photosynthetic bacteria were estimated. For example, the average population density of photosynthetic bacteria was $1.67X10^6$ cells.ml^{-1}. The regeneration times were used to estimate their daily population density ($2.6X10^{10}$ to $8.5X10^{11}$ cells.ml^{-1}). Considering

the average daily consumption of Daphnia pulex ($1.4X10^{10}$ cells.$m.^{-3}day^{-1}$), it was estimated that D. pulex removed 16 to 52% of the daily total photosynthetic bacteria in Crawford Lake.

I feel my estimates of the per cent consumption by D. pulex and D. rosea were overestimates because they did not recognize the importance of the diurnal vertical migration of zooplankton. Edmondson and Litt (1982) reported that Daphnia in the lake ecosystems demonstrate a distinct vertical migration over 24 hour period. They also reported that the high abundance of Daphnia occurred in the hypolimnion during the day light hours and in the epilimnion during the night. No report is available on the diurnal vertical migration of zooplankton in Crawford Lake. However, it was considered that zooplankton in Crawford Lake would demonstrate a typical diurnal vertical migration with high abundance in the deeper waters during day light hours and in the surface waters during the night. It was also assumed that zooplankton in Crawford Lake feed on photosynthetic bacteria during the day light hours and on the algae during the night. As algae and photosynthetic bacteria had an approximately equal contribution to the annual primary production of Crawford Lake (Severn 1982), it was believed that half of the food of filter feeding zooplankton in Crawford Lake were contributed by the algae. Considering the assumption that zooplankton in Crawford Lake feed on photosynthetic bacteria only during the day light hours, it can be suggested that the actual per cent consumption of D. pulex or D. rosea should be only half of that estimated in the study. As a result, instead of 16-52% as stated above, 8-26% of the photosynthetic bacteria were probably consumed by the Daphnia pulex in Crawford Lake. Therefore the corrected per cent consumption of D. pulex and D. rosea ranged from 8-26% and 5.5-17.5% of the total photosynthetic bacteria respectively.

CONCLUSIONS

As a part of the original hypothesis, the result of the in situ feeding experiments made it possible to conclude that a substantial amount of photosynthetic bacteria were contributed to the diet of the filter feeding zooplankton in Crawford Lake, Ontario. It was also concluded that despite the very short regeneration times (3-8 hours) of photosynthetic bacteria their population densities were controlled in part by the grazing of zooplankton. It has been estimated that on the average, the daily consumption of Daphnia pulex and D. rosea ranged from 16 -52% and 11-35% photosynthetic bacteria respectively. As no information is available on the quantitative estimation of zooplankton feeding rates on photosynthetic bacteria, the present investigation increases our understanding of this important process.

In addition, the present data suggest that clearance rates deceased with increasing food concentrations. Ingestion rates were not consistently related to the food concentrations. Both clearance and ingestion rates per unit time for Daphnia pulex were more than that for Daphnia rosea. The relationship between body size of the animals and their filtering rates was similar to that reported in the literature.

Changes in temperature and food appeared to correlate with the temporal fluctuations in the abundance of zooplankton in Crawford Lake. Temperature, dissolved oxygen, and food can be suggested as the major influencing factors associated with the vertical distribution of these zooplankton.

Dissolved oxygen and sulfide concentrations limit the upper boundary attained by the photosynthetic bacteria (Northcote and Halsey 1969; Parkin and Brock 1981b). The lower limit, however, was controlled by light intensity. Below 16m (light intensity below 0.05 μEn.m.s^{-1} $^{-1}$) photosyntehtic bacteria were unable to attain high densities in Crawford Lake.

The seasonal wax and wane of photosynthetic bacteria in Crawford Lake was found to be influenced by changes in dissolved oxygen concentrations, and zooplankton grazing. The population densities of zooplankton and photosynthetic bacteria at the chemocline showed an inverse relationship.

The position of the photosynthetic bacterial layer changed seasonally. A vertical shift of 0.8m (14.5-15.3m) was recorded. It is believed that this shift in the position of the bacterial layer was influenced by the changes in dissolved oxygen and sulfide concentrations at the chemocline.

Aggregation of zooplankton near the bacterial layer was observed during the present investigation. It is believed that this aggregation was stimulated by the food source such as photosynthetic bacteria. This observation was similar to that reported in the literature.

Daphnia and Keratella were found alive and active in the anoxic monimolimnion of Crawford Lake. This observation allowed me to make predictions concerning their ability to tolerate anoxic waters. However, it was not possible to explain how they survive in the anoxic waters. I hope this study will stimulate further investigations into the physiological mechanisms involved in the survivability of these organisms in anaerobic water.

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